River temperature behaviour in changing environments: trends, patterns at different spatial and temporal scales and role as a stressor

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Summary

River/stream water temperature is one of the master water quality parameters as it controls several key biogeochemical, physical and ecological processes and river ecosystem functioning. Thermal regimes of several rivers have been substantially altered by climate change and other anthropogenic impacts resulting in deleterious impacts on river health. Given its importance, several studies have been conducted to understand the key processes defining water temperature, its controls and drivers of change. Temporal and spatial river temperature changes are a result of complex interactions between climate, hydrology and landscape/basin properties, making it difficult to identify and quantify the effect of individual controls. There is a need to further improve our understanding of the causes of spatiotemporal heterogeneity in river temperatures and the governing processes altering river temperatures. Furthermore, to assess the impacts of changing river temperatures on the river ecosystem, it is crucial to better understand the responses of freshwater biota to simultaneously acting stressors such as changing river temperatures, hydrology and river quality aspects (e.g. dissolved oxygen levels). So far, only a handful of studies have explored the impacts of multiple stressors, including changing river temperature, on river biota and, thus, are not well known.

This thesis, thus, analysed the changes in river temperature behaviour at different scales and its effects on freshwater organisms. Firstly, at a regional scale, temporal changes in river temperature within long (25 years) and short time periods (10 years) were quantified and the roles of climatic, hydrological and landscape factors were identified for North German rivers. Secondly, at a reach scale, spatial temperature heterogeneity in a sixth-order lowland river (River Spree) was quantified and the role of landscape factors in inducing such heterogeneity was elucidated. Thirdly, at a site scale, short-term behavioural responses (namely drift) of three benthic invertebrate species to varying levels of water temperature, flow, and dissolved oxygen, and to combinations of those factors were experimentally investigated.

Results from this thesis showed that, at a regional scale, the majority of investigated rivers in Germany have undergone significant annual and seasonal warming in the past decades. Air temperature change was found to be the major control of increasing river temperatures and of its temporal variability, with increasing influence for increasing catchment area and lower altitudes (lowland rivers). Strongest river temperature increase was observed in areas with low water availability. Other hydro-climatological variables such as flow, baseflow, NAO, had significant contributions in river temperature variability. Spatial variability in river temperature trend rates was mainly governed by ecoregion, altitude and catchment area via affecting the sensitivity of river temperature to its local climate. At a reach scale as well, air temperature was the major control of the temporal variability in river temperature over a period of nine months within a 200 km lowland river reach. The spatial heterogeneity of river temperature in this reach was most apparent during warm months and was mainly a result of the local landscape settings namely, urban areas and lakes. The influence of urban areas was independent of its distance from the river edge, at least when present within 1 km. Heat advected from upstream reaches determined the base river temperature while climatological controls induced river temperature variations around that base temperature, especially below lakes. Riparian buffers were not found to be effective in substantially moderating river temperature in reaches affected by lake warming due to the dominant advected heat from the upstream lake. Experimental investigation indicated that increasing water temperature had a stronger short-term effect on behavioural responses of benthic invertebrates, than simultaneous changes in flow or dissolved oxygen. Also, increases in water temperature was shown to affect benthic invertebrates more severely if accompanied by concomitant low dissolved oxygen and flow levels, while interactive effects among variables vary much among taxa.

These results support findings of other studies that river warming, similar to climate change, might be a global phenomenon. Within Germany, lowland rivers are the most vulnerable to future warming, with reaches affected by urbanization and shallow lentic structures being more vulnerable and, therefore, requiring urgent attention. Furthermore, river biota in lowland rivers is particularly susceptible to short-term increases in river temperature such as heat waves. Plantation of riparian buffers, a widely recognized practice to manage climate change effects, in the headwater reaches can be suggested to mitigate and prevent future warming of lowland rivers in general and also throughout river basins, as river temperature response in lowland catchments is a culmination of local and upstream conditions. However, further river temperature increase in lowland river reaches within or close to urban areas and shallow lentic structures will be more difficult to mitigate only via riparian shading and would require additional measures.

Zusammenfassung

Die Wassertemperatur ist ein zentraler Wasserqualitätsparameter, der eine Vielzahl verschiedener biogeochemischer, physischer und ökologischer Prozesse sowie Ökosystemfunktionen von Flüssen steuert. Das Temperaturregime vieler Flüsse wurde bereits nachhaltig durch Klimawandel und andere anthropogene Einflüsse verändert und beeinflusst den chemischen und ökologischen Zustand der Flüsse. Angesichts dieser Bedeutung, haben bereits mehrere Studien die beteiligten Prozesse, Steuergrößen und anthropogenen Überprägungen der Wassertemperatur untersucht. Zeitliche und räumliche Temperaturänderungen resultieren aus einer komplexen Wechselwirkung zwischen Klima, Hydrologie und Einzugsgebietseigenschaften. Die Identifikation und Quantifizierung der Effekte einzelner Steuergrößen ist dementsprechend schwierig. Trotz früherer Studien besteht ein weiterer Forschungsbedarf um die Ursachen der raum-zeitlichen Heterogenität von Wassertemperaturen und ihrer maßgebenden Steuerungsprozesse vollständig zu verstehen. Darüber hinaus ist es entscheidend die Reaktionen von Süßwasserorganismen auf gleichzeitig wirkende Stressoren wie veränderte Wassertemperatur, Hydrologie und Wasserqualitätsaspekte (z.B. Gehalt an gelöstem Sauerstoff) besser zu verstehen um die Bedeutung von Temperaturregimeänderungen vollständig erfassen zu können. Bisher haben nur wenige Studien die Auswirkungen multipler Stressoren, einschließlich der Änderung der Wassertemperatur, auf Süßwasserorganismen untersucht.

Die vorliegende Arbeit adressiert sowohl Temperaturregimeänderungen als auch deren Wirkung auf Süßwasserorganismen auf verschiedenen Skalen. Im ersten Teil werden regionale Wassertemperaturänderungen für lange (25 Jahre) und kurze Zeiträume (10 Jahre) quantifiziert. Dabei werden die Bedeutung von Klima, Hydrologie und Einzugsgebietseigenschaften für Flüsse im Norddeutschen Tiefland identifiziert. Im zweiten Teil der Arbeit wird die Heterogenität zwischen Wassertemperaturänderungen einzelner Flussabschnitte der Spree quantifiziert und mit verschiedenen Einzugsgebietseigenschaften in Bezug gesetzt. Im dritten Teil werden kurzfristige Verhaltensreaktionen (Drift) von drei benthischen wirbellosen Arten, aufgrund einzelner und kombinierter Änderungen von Wassertemperatur, Strömung und dem Gehalt von gelöstem Sauerstoffs experimentell untersucht.

Die Ergebnisse der vorliegenden Arbeit zeigen, dass auf regionaler Ebene, die Mehrheit der untersuchten Flüsse in Deutschland in den vergangenen Jahrzehnten einer signifikanten jährlichen als auch saisonalen Erwärmung unterlag. Die Veränderung der Lufttemperatur ist hierbei die Hauptsteuergröße veränderter Wassertemperaturen und ihrer zeitlichen Variabilität, wobei der Einfluss mit der Einzugsgebietsgröße und tieferen Lagen (Tieflandflüsse) zunimmt. Die stärkste Zunahme der Wassertemperatur wurde in Gebieten mit geringer Wasserverfügbarkeit festgestellt. Aber auch andere hydroklimatische Parameter wie Abfluss, Basisabfluss, NAO, haben einen signifikanten Einfluss auf die Variabilität der Wassertemperatur. Die räumliche Variabilität der Temperaturänderungsraten in Flüssen wird hauptsächlich durch die Klimasensitivität eines Gewässers bestimmt und durch die Ökoregion, Höhe und Einzugsgebietsgröße beschrieben. Auch für den 200 km langen Abschnitt der Spree erklärte, während eines neun-monatigen Messprogramms, die Lufttemperatur maßgeblich die zeitliche Variabilität der Wassertemperatur. In dem untersuchten Abschnitt der Spree wird die räumliche Heterogenität der Wassertemperatur, insbesondere während der warmen Monate, im Wesentlichen durch die lokalen Gegebenheiten (urbane Gebiete und Seen) erklärt. Der Einfluss urbaner Gebiete konnte hierbei unabhängig von der jeweiligen Entfernung (max. 1 km) vom Flussufer festgestellt werden. Insbesondere unterhalb von Seen, wird die mittlere Wassertemperatur eines Gewässerabschnitts hauptsächlich durch die advektiv mit dem Abfluss zugeführte Wärme bestimmt, wohingegen Schwankungen um die mittlere Temperatur maßgeblich durch klimatologische Größen gesteuert werden. Hierbei zeigte sich, dass in Gewässerabschnitten unterhalb von Seen, die advektiv zugeführte Wärme, deutlich dominiert und das Vorhandensein von Gewässerrandstreifen die Wassertemperatur nicht nachweisbar beeinflussen. Die experimentellen Untersuchungen ergeben, dass steigende Wassertemperaturen eine stärkere kurzfristige Änderung der Verhaltensreaktionen des Makrozoobenthos bewirken, als die gleichzeitige Änderung von Abfluss und Sauerstoffgehalt. Die Wirkung erhöhter Wassertemperaturen in Kombination mit geringen Sauerstoffgehalten oder Abflüssen fiel in der Regel stärker aus, unterschied sich in seiner Wirkung jedoch teilweise erheblich zwischen den Arten.

Diese Ergebnisse unterstützen Aussagen anderer Studien, dass die Wassertemperaturerhöhung in Flüssen, ähnlich wie der Klimawandel, ein globales Phänomen ist. In Deutschland sind Tieflandflüsse, insbesondere wenn sie urban geprägt sind oder flache Seen enthalten, am ehesten für einen Temperaturanstieg empfänglich. Sie stellen somit

besonders gefährdete Systeme dar und benötigen einer besonderen Aufmerksamkeit. Darüber hinaus sind Süßwasserorganismen in Tieflandflüssen besonders anfällig für einen kurzfristigen Anstieg der Wassertemperatur durch beispielsweise Hitzewellen. Der Effekt von Gewässerrandstreifen zur Abschwächung von klimawandelbedingten Wassertemperaturanstiegen ist hinlänglich bekannt. Dabei können sich Gewässerrandstreifen im Oberlauf nicht nur lokal positiv auf das Temperaturregime, sondern auch auf unterhalb gelegene Gewässerabschnitte auswirken. Die Minderung eines zukünftigen Wassertemperaturanstieges in urbanen und durch Flachseen geprägten Tieflandflüssen mittels Gewässerrandstreifen ist schwer erreichbar und wird die Implementierung weiterer Maßnahmen erfordern.

Thesis outline

This thesis is composed of three manuscripts that are either accepted for publication, or ready to be submitted to peer-reviewed journals. Each manuscript has an introduction, methodology, results and discussion and forms a chapter of the thesis. A general introduction section provides the general context of the thesis and the results are discussed coherently as the general discussion section. The layout of the three manuscripts was modified and figures and tables were renumbered through the text to ensure a consistent layout throughout the entire thesis. The references of the general introduction, each manuscript, and general discussion were merged in an overall reference section. The research aims of Chapters 2, 3 and 4 are described in Paragraph 1.4.

Chapter 1:

General introduction

Chapter 2:

Arora R, Tockner K, Venohr M. (submitted to Hydrological Processes). Changing river temperatures in Northern Germany: trends and drivers of change.

Author Contributions:

R. Arora designed the study, analysed the data and compiled the manuscript. K. Tockner and M. Venohr co-designed the study and contributed to the text.

Chapter 3:

Arora R, Toffolon M, Tockner K, Venohr M. (to be submitted) Influence of landscape variables in inducing reach-scale thermal heterogeneity in a lowland river.

Author Contributions:

R. Arora designed the study, organized and performed field work, analysed the data and compiled the manuscript. M. Toffolon and M. Venohr co-designed the study and contributed to the text. K. Tockner co-designed the study.

Chapter 4:

Arora R, Pusch MT, Venohr M. (to be submitted) Interactions between effects of experimentally altered water temperature, flow and dissolved oxygen levels on aquatic invertebrates.

Author Contributions:

R. Arora designed the study, organized and performed field and laboratory work, analysed the data and compiled the manuscript. M.T. Pusch co-designed the study and contributed to the text. M. Venohr co-designed the study.

Chapter 5:

General discussion

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1. General introduction

1.1 River temperature: importance in ecosystem functioning and research history

Rivers are hierarchical systems (Montgomery, 1999) in which physical variables such as water temperature, channel area, velocity, flow volume, are present in a continuous gradient of conditions (river continuum concept, Vannote *et al.*, 1980). Among these various variables, river temperature is a physical property of prime importance as it controls physicochemical and ecological processes within freshwater ecosystems. River/stream temperature[2] strongly governs the distribution, abundance (Haidekker and Hering, 2008; Wenger *et al.*, 2011a) and life cycle characteristics such as growth, emergence, metabolism and survivorship (Watanabe *et al.*, 1999; Chadwick and Feminella, 2001, Schindler *et al.*, 2005; Wehrly *et al.*, 2007) of freshwater species. It also controls river metabolism rates (Young and Huryn, 1996; Alvarez and Nicieza, 2005), trophic relationships (Kishi *et al.*, 2005) and food web composition (Woodward *et al.*, 2010b) within rivers. It has a major influence on physical characteristics such as vapour pressure, surface tension, density and viscosity (Stevens *et al.*, 1975) and chemical reaction rates (Brezonik, 1972), which in turn influence primary production and decomposition rates (Friberg *et al.*, 2009; Dang *et al.*, 2009; Woodward *et al.*, 2010a). These processes consequently influence dissolved oxygen concentrations (Sand-Jensen and Pedersen, 2005), nutrient cycling (Ducharne, 2008) and litter processing (Bärlocher *et al.*, 2008); all of which contribute to river ecosystem health (Norris and Thoms, 1999). Given its importance, it is crucial to have a clear understanding of the dynamics of river temperature behaviour (Caissie, 2006).

First reported river temperature measurements date back to 1799, which were made on the River Nile during the Napoleonic expedition to Egypt (Webb *et al.*, 2008). Earliest scientific studies on river temperature appeared around 1960 and mainly aimed to understand the influence of river water temperature on the habitat use and occurrence patterns of cold-water adapted fishes such as salmonids (Benson, 1953; Gibson, 1966; Edington, 1966), the factors governing river thermal processes (Macan, 1958; Ward, 1963), the effects of forest harvesting on river temperature (Gray and Edington, 1969; Brown and Krygier, 1970) and to predict river temperature using heat balance models (Brown, 1969; Morse, 1970). Ever since,

[2] Throughout the thesis, the terms river temperature and stream temperature have been used synonymously

the number of river temperature studies has continuously increased, particularly after 1990 (Hannah *et al.*, 2008b; Fig. I.1). Much of the research until now has focused on understanding river temperature behaviour, direct/indirect impacts of environmental change on river temperature and river temperature modelling (Hannah *et al.*, 2008b). More recently, exploring the past and future trends of river temperature and the influence of climate change and human impacts on these trends has gained interest (Webb *et al.*, 2008; Isaak *et al.*, 2012; Orr *et al.*, 2014; Rice and Jastram, 2015). Several reviews of river temperature research exist in literature. These reviews give a gist of physical processes and controls driving river temperature variability (Smith 1972; Ward 1985; Caissie, 2006), advances in water temperature modelling (Caissie, 2006; Benyahya *et al.*, 2007), natural drivers and human modifications of river temperature (Poole and Berman, 2001; Caissie, 2006), impacts of forest removal (Moore *et al.*, 2005), thermal heterogeneity and past/future changes in river temperature in general (Webb *et al.*, 2008) and advances in river temperature research in United Kingdom (Hannah and Garner, 2015). These reviews clearly highlight the need to further improve our understanding of the spatial and temporal variability in river temperatures and the underlying governing processes of river temperature change, in order to prevent freshwater ecosystems from further degradation.

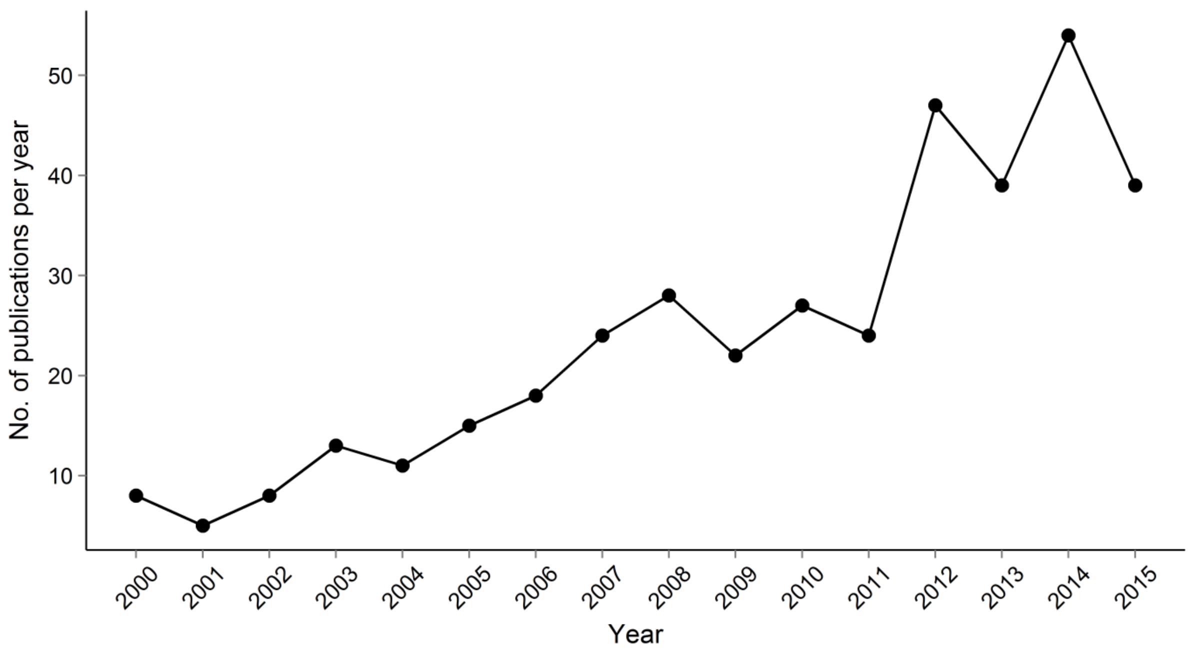

Figure I.1 Studies on river/stream temperature (non-biological) published since 2000. Publications were selected by searching within the ISI Web of Knowledge database using the key words: "stream temperature" OR "river temperature".

1.2 Processes and controls determining river temperatures

River temperature is a complex function of energy and hydrological fluxes occurring at the air-water and riverbed-water interfaces (Hannah and Garner, 2015). Gradients in river temperatures result from spatial and temporal variability in heat fluxes and hydrological processes (Webb, 1996). Thermal energy can be added to a river system via a combination of several processes such as radiation (incident shortwave and longwave), condensation, convective heat transfer and friction at the channel bed and banks and heat conduction from the channel bed. On the other hand, thermal energy can be lost via processes such as reflection of solar radiation, emission of longwave (back) radiation, convection and evaporation (Webb and Zhang, 1997; Hannah *et al.*, 2004; Caissie, 2006). Other components can also be relevant, such as advection through inflows from precipitation, hyporheic exchange, tributaries and groundwater (Caissie, 2006). Heat exchange to a large extent occurs at the air-water interface and, at a smaller extent, at the riverbed-water interface, the significance of which depends on the river characteristics (Webb *et al.*, 2008; Hebert *et al.*, 2011). In general, it is well established that net radiation is the dominant heat source to a river, accounting for more than 70% of heat inputs followed by sensible heat, while evaporation is the dominant sink (Hannah *et al.*, 2004; Webb *et al.*, 2008). However, at the sub-annual scale, the contributions change. During winters, net radiation is the dominant heat sink and sensible heat and bed conduction are the dominant energy sources (Hannah *et al.*, 2004, 2008a). The various energy sources and sinks can be represented in a form of an equation, commonly known as the heat budget equation (Webb and Zhang, 1997) and has been the basis for several river temperature prediction models.

Controls of river temperature are defined by those variables which shape the natural thermal regime of a river via the above mentioned processes. These controls are multivariate and can be external or internal to the river system. External controls such as climate, runoff, highland vegetation, altitude and topographic shade, shape the river's physical environment and control the rate of external heat and water inputs within the catchment. Internal controls such as channel and floodplain morphology, riparian buffer structure, and aquifer stratigraphy, define the river character and geometry, thereby, determining a channel's resistance to warming or cooling and affecting the water temperature response to external temperature controls (Poole and Berman, 2001). These external and internal controls exert their influence over several spatial and temporal scales. Macroscale controls (> 100 km^2; annual to monthly) such as climate, latitude, and altitude, drive the thermal regime of river. Mesoscale controls

(100 km^2- 100 m^2, monthly to daily) such as runoff volume and sources and basin aspect, modify the timing and magnitude of water temperature dynamics, and microscale controls (<100 m^2; monthly to sub-daily) such as channel structure, topographic/riparian shading, hyporheic exchanges and groundwater inputs, further modify the sensitivity of river temperature to the local climate (Imholt *et al.*, 2013; Hannah and Garner, 2015).

Temporal and spatial variations in the magnitude and combination of these controls induce thermal heterogeneity within and among river systems. Interactions between these controls are complex and create different thermal regimes or, in contrast, different combinations of controls can also induce similar thermal regimes (Imholt *et al.*, 2013), making it difficult to disentangle them. Controls causing heterogeneity in river temperature regimes on a catchment, regional and countrywide scale are well studied (Webb *et al.*, 2008). The investigation of controls causing thermal heterogeneity at reach and site scale (vertical and lateral variation in water column) has been receiving renewed attention but needs further research, owing to the complexity of their interactions (Webb *et al.*, 2008).

1.3 Changing river temperatures in changing environments and its implications

1.3.1 Changing river temperatures in changing environments: drivers of change

Humans have substantively altered the structure of river systems and the environmental setting along the course of rivers over time. Installation of dams, water withdrawals, modification of channel structure (e.g., straightening, bank hardening, diking), waste water inputs, the removal of vegetation (highland and riparian), and urbanization, are all examples of ways via which river temperature controls are altered. Global environmental changes, which include the aforementioned human modifications as well climate change, are, therefore, drivers of change of river temperature regimes (Hannah and Garner, 2015). These drivers of change, by modifying the magnitude and combination of controls, can alter the timing or the amount of net heat inputs into a channel, for e.g., by altering the amount of solar radiation (direct impact), and/or by affecting the flow regime of rivers (indirect impact). The resulting effect of these modifications depends on the sensitivity of rivers or their assimilative capacity for heat (such as rivers with low flows) (Poole and Berman, 2001), while such modifications can also alter a river's sensitivity.

Among the various drivers of change, the impacts of riparian vegetation removal on river temperature are the best studied and a comprehensive review on the related findings has been carried out by Moore *et al.* (2005). In general, forest removal, especially without leaving riparian buffers, may elevate maximum water temperatures (up to 8°C) and diurnal range primarily during summer, owing to an increase in solar radiation, wind speed, exposure to air advected from clearings and decreases in relative humidity. Moreover, several studies have shown that rivers need at least 5 to15 years to return to their natural thermal regime after a recovery in riparian vegetation (Moore *et al.*, 2005; Caissie, 2006). In comparison, only a handful of studies have explored the response of river temperature to urbanization (LeBlanc *et al.*, 1997; Nelson and Palmer, 2007; Hester and Bauman, 2013; Somers *et al.*, 2013; Xin and Kinouchi, 2013; Booth *et al.*, 2014). Increased air and land surface temperatures (up to 10°C), wastewater input, runoff from warmed impervious surfaces during precipitation, contribute to elevated river temperatures and heat surges within cities (Nelson and Palmer, 2007; Somers *et al.*, 2013). River temperature changes in response to flow reductions (water abstractions) and releases below reservoirs have received increasing interest (Webb *et al.,* 2008). Artificial reductions or increases in flow alter the assimilative thermal capacity of the river, resulting in an increased occurrence of high temperature events and increases in temperature minima, respectively (Webb *et al.*, 2008; Hannah and Garner, 2015).

Drivers of change can also alter long-term river temperature dynamics. Recently, several studies have investigated the factors responsible for long-term changes in river temperature regimes. Majority of these studies have reported an increase in river temperature during the past decades (Hari *et al.,* 2006; Webb and Nobilis, 2007; Kaushal *et al.*, 2010; van Vliet *et al.*, 2011; Isaak *et al.*, 2012; Markovic *et al.*, 2013; Orr *et al.*, 2014; Rice and Jastram, 2015), which have often been attributed to changes in air temperature. In some cases, long-term increase in river temperature have also been attributed to urbanization (Kinouchi *et al.*, 2007), presence of dams (Petersen and Kitchell, 2001) as well as land use changes and water diversion (Arismendi *et al.*, 2012). Hence, there is a growing consensus on the fact that attribution of river temperature changes solely to climate change is difficult, given the simultaneous impacts of several drivers of change on river temperature. Additionally, as the different drivers of change act at several spatiotemporal scales, a generalization about the magnitude and the causes of river temperature change remains a challenge (Webb *et al.*, 2008; Hannah and Garner, 2015).

1.3.2 Implications of changing river temperature on freshwater organisms

Together, impacts of climate change and those arising from direct human interferences have already modified thermal and hydrological regimes of rivers and are expected to continue to do so in the future (van Vliet *et al.*, 2013). Modifications of thermal and hydrological regimes pose a significant imminent threat to the survival and diversity of freshwater species, and ultimately to river ecosystem health (Ormerod *et al.,* 2010; Wooster *et al.,* 2012; Floury *et al.,* 2013; Markovic *et al.,* 2014). The observed increases in river temperature, especially when accompanied with altered flows, trigger various cascading effects on a number of physical, chemical and biological processes in river ecosystems (Pusch and Hoffmann 2000; Whitehead *et al.,* 2009) as well as on the physiology of freshwater biota and composition of communities. River warming has been shown to result in an earlier onset of adult insect emergence, increased growth rates, decreases in body size at maturity, altered sex ratios, decreased densities (Hogg and Williams, 1996), increased taxonomic richness (Jacobsen *et al.,* 1997) and shifts in community structure of invertebrates (Daufresne *et al.*, 2004; Durance and Ormerod, 2007; Haidekker and Hering, 2008). More recently, Woodward *et al.* (2010b) observed increases in food chain length with increasing water temperature, with fishes (e.g. brown trout) having a higher trophic status in warmer rivers as compared to colder rivers. Key ecosystem processes such as primary production and decomposition rates, also rise significantly with temperature (Bärlocher *et al*., 2008; Friberg *et al*., 2009) and consequently, affect other water quality variables such as decreases in dissolved oxygen levels (Johnson and Johnson, 2009). An increase in the frequency of extreme hydro-climatic events such as heat waves, droughts or floods can also have strong impacts on freshwater ecosystem processes and ecology. Both maximum temperatures and the frequency of warm spells (or heat waves i.e., at least five days of consecutively high maximum temperature) have increased between 1951 and 2010 and are assumed to increase further in the future (IPCC, 2013). Such events are likely to have profound and complex consequences for aquatic ecosystems (Lake, 2011) by causing loss of favourable habitat, limiting species dispersal, reducing resilience and causing local extinction of heat-sensitive taxa (Leigh *et al.*, 2014).

Since climate change and human interferences affect several aspects of river water quality at once, concomitant changes in more than one water quality parameter, such as dissolved oxygen levels, flow, nutrient concentrations, will induce synergistic or antagonistic impacts that will result in complex ecological responses. Until recently, only a handful of studies have investigated the long-term and short-term impacts of such concomitant changes in water quality parameters on freshwater macroinvertebrate communities (Daufresne *et al.*, 2004; Burgmer *et al.*, 2007; Durance and Ormerod, 2009; Floury *et al.*, 2013; Vaughan and Ormerod, 2014; Piggott *et al.*, 2015). Particularly, as the interactive effects among increasing water temperature and other stressors are less explored (Woodward *et al.*, 2010a; Piggot *et* *al.*, 2015), there is a need to observe and quantify the impacts of multiple stressors (including water temperature) on the response of freshwater macroinvertebrate communities.

1.4 Research gaps, aims and structure of the thesis

Despite the rich literature on river temperature dynamics and the various factors controlling the dynamics, major research gaps remain, particularly with respect to spatial and temporal heterogeneity in river temperature (Webb *et al.*, 2008; Hannah and Garner, 2015). At broad spatial and temporal scales, few studies have investigated past changes in river temperature and most of them have been carried out for North American rivers (Kaushal *et al.*, 2010; Issak *et al.*, 2012; Arsimendi *et al.*, 2012; Caldwell *et al.*, 2014; Rice and Jastram, 2015). In Europe, the most comprehensive study so far focused on river temperature trends at 2773 sites across England and Wales (Orr *et al.*, 2012). Other studies on river temperature trends in Europe (e.g., Webb and Nobilis 1995; Hari *et al.*, 2006) cover only a few sites or rivers. A generalization and comparison of the derived river warming trends and its causes remain a challenge given the variety of potential controls and drivers of change, differences in data quality/quantity and, also, due to differences in river sensitivities to the local climate (Hannah and Garner, 2015). At the reach scale, although substantial research has focused on the effects of riparian buffers on river temperature responses, relatively few studies have explored river temperature responses to urbanization. In particular, no study has yet investigated the role of landscape variables, such as different land use covers, in inducing within-river or reach-scale heterogeneity in water temperatures. Additionally, a majority of the studies on river thermal dynamics has been done for highland rivers (Broadmeadow *et al.*, 2011) as opposed to lowland rivers. Regarding the impacts of changing river temperature on freshwater biodiversity in a multiple stressor context, the responses of riverine biota to concomitant changes in different parameters have not been well explored (Woodward *et al.*, 2010a). More notably, none of the existing studies have studied and compared the relative impacts of increased water temperature, low flow and low DO levels on invertebrates by combined application of those stressors.

More importantly, hardly any research on river temperature changes and dynamics has been done for German rivers. Markovic *et al.* (2013) quantified the variability, magnitude, and extent of temperature alterations at different time scales for 11 sites along the River Elbe and four sites along the River Donau in Germany, while Koch & Grünewald (2010) developed and assessed the performance of daily river temperature regression models for two stations on

River Elbe. In Germany, the average annual air temperature has increased by about 1.3°C between 1881 and 2014 and the last 14 years have been the warmest so far (DWD, 2015). Also, average annual flow has increased for many rivers since 1950 (Bormann, 2010), mainly due to increasing winter flows, while summer flows have exhibited decreasing trends (Bormann, 2010; Stahl *et al.*, 2010). Future climate projections predict significant warming across Germany with an increase in air temperature of 1.6 to 3.8°C by the year 2080 (Zeibsch *et al.*, 2005). Moreover, extreme low flow conditions, especially in summer, are expected to become much more common, especially in eastern Germany (UBA, 2010; Huang *et al.*, 2012). Finally, more than 90% of the rivers are in a moderate or bad ecological state (UBA, 2013), which makes it even more urgent to understand the past changes as well as the causes of spatiotemporal heterogeneity in river temperature behaviour and its role as a stressor.

Thus, this thesis aims to investigate spatial and temporal heterogeneity in river temperature at large and small scales for German rivers as well as the impact of increasing river temperature on freshwater invertebrates in a multiple stressor context. The specific aims and objectives of the thesis are as follows:

1) ***Quantify the trends in river temperature and drivers of change across Northern Germany (Chapter 2):*** In this chapter, I analysed the trends in river temperature within 1985-2010, for 475 sites in Northern Germany and the role of several hydro-climatological variables (air temperature, flow, NAO) and landscape variables (altitude, land use change, land cover, catchment area, ecoregion, river type). This will help gain a clearer understanding of individual and combined influences of hydro-climatological and landscape variables in inducing spatially and temporally variable river temperature changes.
2) ***Observe and quantify spatial variation in water temperatures in a lowland river and the role of landscape variables (Chapter 3)***: In this chapter, I observed spatial thermal heterogeneity in a ~200 km reach (20 sites) of a lowland river in northeast Germany (River Spree) for a period of nine months (January-September 2014) which flows through several land use types (forest, agricultural and urban areas). I quantified the heterogeneity in the heat budget and through a semi-empirical model and explored the role of hydro-climatological variables, land use types, lakes and river aspect in causing the observed thermal heterogeneity.
3) ***Influence of altered water temperature on aquatic invertebrates in a multiple stressor context (Chapter 4)***: In this chapter, I experimentally investigated the

behavioural responses, namely drift, of three river macroinvertebrate species [Odonata (*Calopteryx splendens*), Trichoptera (*Hydropsyche pellucidula*), Amphipoda (*Dikerogammarus haemobaphes*)] to varying levels of water temperature, flow and dissolved oxygen, and to combinations of those factors. The test animals were obtained from the River Spree, a sixth-order lowland river in northeast Germany.

2. Changing river temperatures in Northern Germany: trends and drivers of change

Roshni Arora, Klement Tockner and Markus Venohr

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3. Influence of landscape variables in inducing reach-scale thermal heterogeneity in a lowland river

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3.1 Abstract

Identifying the role of landscape variables, especially land use, in inducing reach-scale thermal heterogeneity in river/stream temperature represents an ongoing task. The present study investigated the temporal and spatial heterogeneity of stream temperature (ST) and the role of landscape variables at 20 locations within a ~200 km reach of the intensively managed lowland river (River Spree) in northeast Germany over a 9-month period. The results showed the presence of thermal heterogeneity within the reach, which was most apparent during warmer months and was mainly affected by the presence of urban areas and lakes. Quantification of this effect in the heat budget was estimated via a residual heat flux term E_r. Correlations of mean ST and E_r with hydro-climatological and landscape variables at different temporal and spatial extents corroborated the above results, showing that the influence of urban areas was independent of its distance from the river edge, at least within 1 km. Forest-induced microclimates also had a significant effect in moderating ST, but the effective spatial width was not clear. Furthermore, especially for lake influenced reaches, it was determined that the upstream advected heat determined the base ST, while climatological variations induced ST variations around that base temperature. Application of a semi-empirical model allowed for capturing the spatial heterogeneity in the reach and, as compared with regression models, delivered a much better performance in predicting ST with the same input data, questioning the widespread application of regression models.

3.2 Introduction

Water temperature governs several key physical, chemical and biological processes and is crucial for sustaining and providing various river ecosystem functions (Webb 1996; Johnson and Johnson, 2009; Friberg *et al.*, 2009; Johnson *et al.*, 2014). Several river systems around the world have already warmed in the past few decades (Kaushal *et al.*, 2010; van Vliet *et al.* 2011; Isaak *et al.*, 2012; Markovic *et al.*, 2013; Rice & Jastram, 2015; Chapter 2) and are predicted to continue warming in the future (van Vliet *et al.*, 2013). Increasing water temperature has detrimental impacts on water quality and habitat suitability for freshwater species, thereby having ecological as well as socio-economic consequences (EEA, 2008b; van Vliet *et al.*, 2013). Large spatial heterogeneity in stream/river temperature could act as thermal migration barriers for freshwater species, reducing connectivity and harbouring different community compositions within the same reach (Sponseller *et al.,* 2001; Kelleher *et al.,* 2012). Accordingly, an increasing number of studies are being conducted to understand the controls of thermal dynamics of rivers, to delineate the causes of heterogeneity among systems and to identify the factors behind observed widespread river warming (Johnson *et al.*, 2014).

Water temperature is a function of energy and hydrological fluxes at the air and riverbed interfaces of a river (Hannah and Garner, 2015). Heat is added to or lost from a river through mechanisms such as radiation, conduction, convection and advection (Webb and Zhang, 1997). In general, net radiation is the dominant source of heat to a river, accounting for more than 70% of heat inputs (Webb *et al.*, 2008). Multiple controls (such as climate, flow, land use) can influence one or more of these processes at several spatiotemporal scales and induce thermal heterogeneity within and across river systems (Imholt *et al.*, 2013; Hannah and Garner, 2015). The role of land use alteration in stream temperature modification, especially removal of forest canopy, has been explored extensively (Moore *et al.*, 2005; Malcolm *et al.*, 2008). Riparian buffer harvesting increases the amount of incident solar radiation along with wind speed, causing an increase (up to 8°C) in maximum stream temperatures (Moore *et al.*, 2005). In comparison, only a handful of studies have yet explored stream temperature response to presence of urban areas (LeBlanc *et al.*, 1997; Nelson and Palmer, 2007; Somers *et al.*, 2013; Booth *et al.*, 2014). Increased air and land surface temperatures (up to 10°C), wastewater additions, runoff from warmed impervious surface during precipitation contribute to elevated stream temperatures and heat surges within cities (Nelson and Palmer, 2007; Somers *et al.*, 2013). Presence and spatial location of different land use types, such as forest, urban and agricultural areas, in a watershed or along a river, can be expected to directly or indirectly lead to creation of thermally heterogeneous reaches in rivers, by either altering the amount of incident solar radiation and/or by inducing different hydrologic responses in rivers (Poff *et al.,* 2006; Sun *et al.*, 2014). Most of the studies considering land use as an influencing factor or a determinant of stream temperature generally include forest as a variable (Pedersen and Sand-Jensen, 2007; Hrachowitz *et al.*, 2010; Broadmeadow *et al.*, 2011; Mayer, 2012; Imholt *et al.*, 2013; Hebert *et al.*, 2014), whereas only few have studied the effect of other land use types in causing different river thermal environments. For example, Chang *et al.* (2013) found percent share of forest cover to be a better predictor of maximum stream temperature in Columbia River basin than urban, agriculture or grassland cover. A modelling study by Sun *et al.* (2014) also found that reforestation of an urbanized area had a more pronounced effect on stream temperature than urbanization of a forested area, suggesting a dominant influence of riparian vegetation. Kaushal *et al.* (2010) and Rice and Jastram (2015) suggested more rapid long-term increases in stream temperature in urban areas than in other land use types for several North American rivers. Also, thermal sensitivity of small urban streams has been observed to be higher than of rural or forested streams in Pennsylvania (Kelleher *et al.*, 2012). However, majority of these studies have been conducted at large spatial scales (basin/watershed). To our knowledge, no study has yet investigated within-stream or reach-scale heterogeneity in water temperature of a river flowing through different land-use types. Hence, understanding drivers of thermal heterogeneity in watercourses over a range of scales still presents an ongoing challenge (Webb *et al.*, 2008).

With this rationale, we conducted a reach scale study to observe and quantify variation in water temperatures in a lowland river in north-eastern Germany, flowing through three major land use types, namely forest, agricultural and urban areas. Lowland river systems are usually more populated than upland areas (Wolanski *et al.*, 2004) and, hence, bear the cumulative impacts of numerous on-site stressors (such as climate change, channelization, impoundments, water additions/withdrawals, land use change) as well as the alterations in the upstream reaches (Floury *et al.*, 2013). They have also received lesser attention than highland rivers in terms of thermal dynamics investigations, as many studies on lowland rivers involve single location observations towards the lower end of major river systems (Broadmeadow *et al.*, 2011). We specifically addressed the following questions:

1) Is there any spatial heterogeneity in stream temperatures (ST) along the reach and, if present, can it be quantified in the heat budget?
2) Is the observed spatial thermal heterogeneity related to the spatial location of land use types along the reach? At what temporal scale (daily, monthly, entire period) and lateral spatial extent is the impact of land use types most apparent?
3) How do other landscape variables such as lakes or stream aspect and hydro-climatological variables contribute to the thermal heterogeneity?
4) How well can a semi-empirical model capture the dominant controls of ST in the reach?

In addition, given the need to move beyond regression models owing to their poor performance (Arismendi *et al.*, 2014), we also compared the performance of regression models with a semi-empirical hybrid model in predicting stream temperature (Toffolon and Piccolroaz, 2015), based on air temperature as input.

3.3 Materials and methods

3.3.1 Study area

The River Spree is a sixth-order river with a total catchment area of 10,100 km^2 and lies in the east Elbe catchment in north-eastern Germany. It originates at 390 m above sea level (asl) in the Lusatian Mountains near the Czech border. It has typical hydrological and ecological features of a lowland river of the central plains. The river flows through several lakes on its 380 km long course which terminates in Spandau, Berlin, as it merges with the River Havel at 30 m asl. For this study, the ~200 km long lower section of the River Spree (between Leipe, Brandenburg and Spandau, Berlin) was considered (Fig. III.1). The Spree catchment upstream of Berlin has a relatively high percentage of forest at 41.5%, 43.4% crop fields, 4.6% settlements and 2.2% surface waters (Tockner *et al.*, 2009). In this lower section, the river flows through the Glogów-Baruth glacial valley and the river slope reaches a minimum (average slope range 0.001 - 0.13%) (Kozerski *et al.*, 1991). Due to the flat orography and unconsolidated bedrock in most of the catchment, the flow regime of the Spree is highly deteriorated in comparison to other rivers of similar size in Central Europe. The mean discharge for the year 2014 near Fehrow was 4 m^3s^{-1} whereas near Spandau it was 23 m^3s^{-1}. The specific runoff between Cottbus and Berlin ranged from 2.4 - 4.1 L km^{-2} s^{-1} during 1997-2007 (Tockner *et al.*, 2009). The annual discharge regime is regulated and smoothed by reservoirs in the upper part and weirs immediately downstream of lakes and in smaller tributaries. Majority of the lakes and reservoirs in this region are shallow and have low landscape gradients (Kozerski *et al.*, 1991).

Climate in the entire catchment is mostly sub-continental with relatively low annual precipitation and hot and dry summers. Mean annual temperature at Lindenberg, which is in the middle of the lower catchment, was 9.2°C (time period 1981-2010). It is one of the driest regions within Germany with precipitation up to 500 mm (below 576 mm in the period 1981-2010 at Lindenberg).

Despite low water availability in the catchment, this lower section of River Spree has multiple uses, such as drinking water supply, recreation, coolant for power plants, receiving tertiary-treated wastewater, waterway for navigation, and is thereby subject to several pressures. Also, it has undergone severe transformations due to lignite mining activities in the past, making it one of the most intensively managed rivers of the world (Tockner *et al.*, 2009).

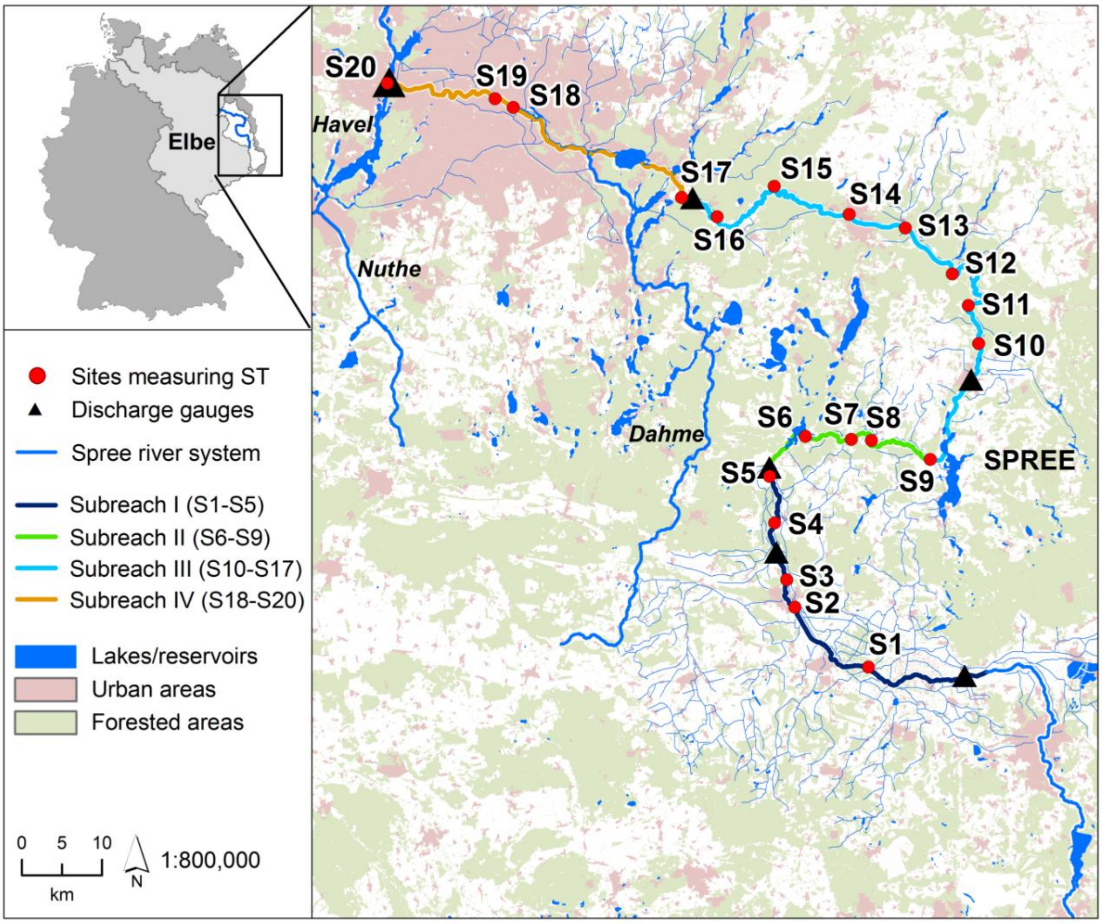

Figure III.1 Maps showing the location of the study area, stream temperature (ST) measuring locations, and the thermally heterogeneous sub-reaches. Stream temperature measuring locations are numbered corresponding to their IDs (Table III.2).

3.3.2 Dataset

Stream temperature (ST) was recorded at 15 min intervals at 20 locations (19 reaches) on River Spree over a distance of 195 km (Fig. III.1). The recording period was from 1 January 2014 to 31 December 2014. The temperature was recorded using Gemini TinyTagPlus data loggers (model TG-4100) with an internal encapsulated thermistor. Stated precision for the loggers is ±0.2°C. The loggers were cross-calibrated prior to installation and were found to be within ±0.1°C of each other. Due to dewatering or delays in data downloading, only 13 out of 20 loggers had data for the entire year. So, for the correlation and regression analysis data up till 15 September 2014 (available for all loggers) were used, whereas for model applications entire year's data were used where available.

Table III.1 Hydro-climatological and landscape variables considered in the analysis.

Hydro-climatological variables	**Landscape variables**
Air temperature [°C]	Forest area in 50 m buffer (F_50) [%]
Solar radiation [J cm^{-2}]	Forest area in 100 m buffer (F_100) [%]
Relative humidity [%]	Forest area in 500 m buffer (F_500) [%]
Wind velocity [m s^{-1}]	Forest area in 1000 m buffer (F_1000) [%]
Atmospheric pressure [mbar]	Agricultural area in 50 m buffer (F_50) [%]
Cloud cover [okta]	Agricultural area in 100 m buffer (F_100) [%]
Discharge [m s^{-3}]	Agricultural area in 500 m buffer (F_500) [%]
	Agricultural in 1000 m buffer (F_1000) [%]
	Urban area in 50 m buffer (F_50) [%]
	Urban area in 100 m buffer (F_100) [%]
	Urban area in 500 m buffer (F_500) [%]
	Urban area in 1000 m buffer (F_1000) [%]
	Lake distance [m]
	Stream azimuth (aspect) [°]

Hourly data for climatological variables such as air temperature, relative humidity, wind velocity, atmospheric pressure, cloud cover and shortwave radiation were downloaded from the Deutsche Wetter Dienst (DWD, www.dwd.de) for the relevant period. This data were available at five locations for air temperature and relative humidity whereas only at a single location for the rest of the variables. Therefore, the data of the five stations were averaged across sites for each time step to obtain the air temperature and relative humidity data for the region. Daily discharge (flow) data were obtained from Landesamt für Umwelt, Gesundheit und Verbraucherschutz (LUGV; www.luis.brandenburg.de/) and were available at six locations within the study reach (Fig. III.1).

A total of 14 landscape variables were included in the study and basically comprised of shares (%) of land cover for different buffer widths, lake distance and stream azimuth (aspect) (Table III.1; Fig. SIII.1). Land cover data along the reach were obtained from ATKIS land-use dataset (10 m × 10 m resolution; ADV, Germany). Lake distances and stream azimuth values were calculated from Google Earth. Azimuth was measured as the angle (degrees) that the overall stream channel differed from due south (e.g., due south = 0°, due west = +90°, and due east = -90°) (Arscott *et al.*, 2001). Since elevation was very similar across sites (58-30 m), it was not considered for analysis.

3.3.3 Quantification of contribution of landscape controls in the heat budget

Heat content variations in a river reach was computed using the following energy balance:

$$\frac{d}{dt}\left(\rho\, C_p\, V\, T_w\right) = H_{up} - H_{down} + S\,(E_{atm} + E_r + \Delta E) \tag{1}$$

where T_w is stream temperature, ρ and C_p are density (assumed constant, 997 kg m^{-3}) and specific heat of water (assumed constant, 4179 J kg^{-1} °C^{-1}), V is volume of the reach (m^3), S is the surface area (m^2), H_{up} is the total heat flux entering (W) the volume from the upstream section, H_{down} is the total heat flux (W) going out downstream, E_{atm} is the net exchange per unit surface (W m^{-2}) with atmosphere estimated as an average value for the whole study area. The various heat flux components of E_{atm} (solar radiation, sensible and latent heat flux, evaporation, condensation, etc.) were calculated using the relationships reported in Martin & McCutcheon (1998) (see Appendix C). The value ΔE is a correction factor (W m^{-2}) accounting for global uncertainties in the determination of E_{atm} with the empirical heat budget equations. Moreover, E_r is the remaining energy flux term (W m^{-2}) that is expected to be a contribution of sources other than the exchange with the atmosphere, rescaled with the surface area S. This term is site-specific and is assumed to majorly include the unresolved terms, such as land use- based sources (such as wastewater, urban outflows), inflows from lakes, tributaries and groundwater not explicitly included in H_{up}. Since the solar radiation values were region-based and not site-based, effects of reduced incident solar radiation (reduced heat inputs) in shaded areas are also included in E_r.

Equation (1) was discretized by subdividing the entire reach into computational reaches defined by the location of the ST measuring sites. Each computational reach had a discrete stream temperature $T_{w,i}^k$ (°C, with i the index for space and k for time) in the volume V_i. Assuming steady and uniform hydraulic conditions (i.e., constant discharge, Q (m^3 s^{-1}), or/and cross-section) along a computational reach i, and further assuming that the downstream temperature $T_{w,down} \cong T_{w,i}^k$ (thus considering each computational reach as a completely mixed reactor), the upstream and downstream heat fluxes were calculated as

$H_{up} = \rho C_p Q_i T_{w,i-1}$ and $H_{down} = \rho C_p Q_i T_{w,i}$, respectively. Thus, the temperature change in a river reach can be calculated by the following heat balance:

$$\frac{T_{w,i}^{k+1} - T_{w,i}^{k}}{\Delta t} = \frac{Q_i}{V_i} \left(T_{w,i-1}^{k} - T_{w,i}^{k}\right) + S_i \frac{E_{atm} + \Delta E}{\rho\, C_p\, V_i} + S_i \frac{E_{r,i}}{\rho\, C_p\, V_i}, \qquad (2)$$

where, an explicit Euler scheme was used for the discretization, as a first approximation. The volume was estimated as $V_i = B_i D_i L_i$, where B_i is the river width (m), D_i is the depth (m) and L_i the length (m) of the reach. All the surface heat fluxes were calculated referring to a surface area $S_i = B_i L_i$.

Alternatively, if the temperature changes across space and time are known, equation (2) yields a way to estimate the residual heat term,

$$E_{r,i} = \rho\, C_p\, D_i \left(\frac{T_{w,i}^{k+1} - T_{w,i}^{k}}{\Delta t}\right) - \rho\, C_p\, \frac{Q_i}{B_i L_i} \left(T_{w,i-1}^{k} - T_{w,i}^{k}\right) - E_{atm} - \Delta E\ . \qquad (3)$$

Some assumptions helped us in the interpretation of the residual term E_r (W m^{-2}). Groundwater contributions to ST spatial heterogeneity was assumed to be negligible because water conductivity, an indicator of groundwater inflow (Johnson and Wilby, 2015), was similar at most of the sites (Table III.2). Regarding the influence of tributaries, although there are several small streams or canals flowing into River Spree, not enough information on these inputs was available. Also, there are no major tributaries joining directly with the main river along the study reach, except River Dahme which joins River Spree in its final reach. Hence, tributary contributions were also assumed to be negligible. Ultimately, E_r mainly consists of heat contributions from land-use sources and lake inflows (the latter by means of alterations of the upstream heat flux) within the reach.

For this analysis, the 19 sections in River Spree were analysed in six groups (S1 to S2; S3 to S5; S6 to S9; S10 to S14; S15 to S17; S18 to S20; see Fig III.1) according to the discharge information available. The discharge in each group was assumed to be constant. The calculations were performed using daily averaged values of ST and hydro-climatological variables.

Table III.2 Description of the stream temperature observation sites on River Spree.

Thermally different sub-reaches	Site ID	Name	Distance (km)	Mean ST for entire period	Maximum ST (sub-daily; 15 min)	Time at Maximum ST	Forest Area (% of total in the reach; 50 m wide buffer)	Urban Area (% of total in the reach; 50 m wide buffer)	Distance from the closest lake (km)	Conductivity (µ cm^{-1}; based on daily mean value on 14 Jan 2008)
Sub-reach I	S1	Leipe	0	13.04	24.25	21-07 17:15	30	16	51	947
	S2	Lubben	14	13.06	24.87	21-07 17:30	62	17	65	857
	S3	Hartmannsdorf	18	13.14	25.26	21-07 17:00	32	50	69	822
	S4	Schlepzig	27	13.25	25.30	22-07 18:00	92	2	78	NA
	S5	Leibsch	33	13.32	25.26	22-07 18:15	33	5	84	815
Sub-reach II	S6	Altschadow	42	13.95	27.78	20-07 15:00	13	10	0.5	893
	S7	Werder	49	13.90	26.83	21-07 02:15	19	1	8	NA
	S8	Kosenblatt	52	13.73	27.08	21-07 15:00	23	6	11	NA
	S9	Trebatsch	62	13.77	26.37	21-07 23:15	22	7	21	0.88
Sub-reach III	S10	Radinkendorf	81	14.13	26.88	21-07 16:15	41	13	2	823
	S11	Rassmansdorf	87	14.03	26.41	21-07 16:30	25	2	8	0.84
	S12	Drahendorf	99	13.80	25.77	20-07 16:15	35	3	10	837
	S13	Berkenbrucke	108	13.84	26.59	22-07 11:30	52	5	19	NA
	S14	Furstenwalde	116	13.97	26.79	20-07 15:00	35	65	27	836
	S15	Hangelsberg	129	13.73	26.34	22-07 13:15	38	7	40	NA
	S16	Freienbrink	141	13.81	26.42	20-07 19:00	21	3	52	NA
	S17	Neu zittau	148	13.24	24.79	20-07 18:00	15	9	59	832
Sub-reach IV	S18	Warschauer str	176	14.14	26.59	20-07 18:00	33	53	16	NA
	S19	Jannowitz	179	14.18	26.63	20-07 15:00	0	100	19	824
	S20	Spandau	195	14.52	26.61	20-07 14:45	7	93	35	835

3.3.4 Identification of dominant ST controls

3.3.4.1 Lagrangian model

In order to ascertain the mechanism through which the upstream conditions affect downstream ST and the role of riparian buffer in regulating water temperature, we developed a simple Lagrangian model (Leach and Moore, 2011). In this approach, a reach is divided into a series of segments bounded by nodes (index j). A water parcel having an initial ST (based on measured values) is released from the upstream boundary at each time step. As the water parcel flows downstream from one node to the next (j to $j+1$), the model computes the heat inputs and the consequent change in stream temperature over the stream segment. This can be formally represented as follows:

$$T_w\left(x_{j+1}, t_{k+1}\right) = T_w\left(x_j, t_k\right) + \left(\rho\ C_p\ D_j\right)^{-1} \sum E_l\ \Delta t\ , \quad x_{j+1} = x_j + U_j \Delta t\ , \qquad (4)$$

where, $\sum E_l = E_{atm} + E_r + \Delta E$ represents the sum of all the external heat fluxes acting in the time interval Δt (15 min). In our simulation, the flow velocity U_j was assumed as constant in each segment L_i. Reference values of flow velocity U = 0.2 m/s and depth D = 1 m were estimated by steady-state simulations using the software HEC-RAS (USACE, 2010; http://www.hec.usace.army.mil). The hydrodynamics of the river was characterized assuming a simplified geometry of equivalent rectangular cross-sections having width B = 40 m, as the information on the longitudinal variation of the cross-sections of the river was insufficient. For this analysis, the STs were simulated for site S9 (downstream) starting from the upstream site S6 (located at a lake outlet), for 15 days in July (5/07-31/07), the hottest month of the year.

To determine the influence of upstream conditions, simulations using the Lagrangian model were compared with the simulations from a reduced model based on equation (2) with ST determined locally (hereafter termed "local" Eulerian model) at a site i:

$$T_w(x_i, t_{k+1}) = T_w(x_i, t_k) + \left(\rho\ C_p\ D_j\right)^{-1} \sum E_l\ \Delta t\ , \qquad (5)$$

i.e., neglecting the advected heat fluxes and considering only the local exchange term $\sum E_l$. Additionally, to determine the role of riparian buffer in regulating ST below lakes, STs were simulated using the Lagrangian and the "local" Eulerian model in two scenarios of incident solar radiation inputs, zero (complete shade) and 100% (no shade).

3.3.4.2 Correlations, linear and non-linear statistical modelling

Statistical analyses to describe different aspects of stream thermal dynamics where performed on the basis of mean daily and mean monthly values. To estimate daily contributions of hydro-climatological variables in ST variations at each site, linear regression and generalized non-linear models (spline-smoothing function from the *mgcv* package in R software, where significance of the smooth term was reported) were applied to daily values of ST and hydro-climatological variables. The Durbin–Watson test was used to detect autocorrelation in the linear model residuals and was found to be significant for all variables. In the presence of autocorrelation, the reported R^2 statistics should be interpreted as an upper limit since autocorrelation tends to reduce the sample sizes of the regression models (Johnson *et al.*, 2014). Logistic regression model (Mohseni *et al.*, 1998) was also fitted to air temperature and ST values to compare with linear regression model performance according to the following equation:

$$T_w = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - T_a)}}\,, \tag{6}$$

where T_w is the estimated water temperature, T_a is the measured air temperature, α is the estimated maximum water temperature, μ is the estimated minimum water temperature, γ is a measure of the slope between water and air temperature, and β represents the inflexion point of the curve.

Mean and maximum values of ST (at daily/monthly/entire period time scales) and mean values of E_r (monthly/entire period time scales) were used to calculate Pearson's correlations for the analysis of the role of landscape variables in modifying ST on a reach scale.

3.3.4.3 Semi-empirical hybrid model

Linear and non-linear statistical models might not be the best options to describe and predict ST, especially at fine spatial scales (Arismendi *et al.*, 2014). Given the need to explore better but simple models, an alternative approach to relate ST to air temperature was applied based on the same input variables. The *air2stream* model (Toffolon & Piccolroaz, 2015) represents an adaptation (for rivers) of the *air2water* approach that was successfully applied to predict lake surface temperature as a function of air temperature (Piccolroaz *et al.*, 2013; Toffolon *et al.*, 2014; Piccolroaz *et al.*, 2015). It is based on a lumped heat budget that considers an unknown volume of the river reach, its tributaries (implicitly considering both surface and subsurface water fluxes), and the heat exchange with the atmosphere. The heat budget (equation 1) is simplified until only the dependency on air temperature (as a proxy of the other processes) is retained (please refer to Toffolon and Piccolroaz, 2015 for further details). The model is proposed in five versions, each based on different assumptions, and the versions differ for the number of parameters (from 3 to 8). The 8-parameter version is the full model and incorporates the contribution of discharge. Since the discharge data were not available at all locations, the 5-parameter version of the model was used for this analysis:

$$\frac{dT_w}{dt} = c_1 + c_2 T_a - c_3 T_w + c_4 \cos\left[2\pi\left(\frac{t}{t_y} - c_5\right)\right], \qquad (7)$$

where T_w is the stream temperature, T_a is the air temperature, t is time (in days), t_y is the duration of a year (in days) and c_1 to c_5 are constant parameters (corresponding to a_1, a_2, a_3, a_6, and a_7 of the original formulation in Toffolon and Piccolroaz, 2015). The values of these parameters are estimated through calibration, so that neither the geometrical characteristics of the river reach (length, volume, area, etc.) nor the roles of specific heat inputs (e.g., internal friction, along-reach inflows) are explicitly specified. The second term on the right hand side of equation (7) represents the effect of air temperature (as a proxy) on the net heat flux. The fourth term on the right hand of equation represents the heat fluxes associated with inflows, representing the contribution of factors (such as groundwater, land use, lakes) which modify ST dynamics but are of difficult determination.

If we divide equation (6) with the coefficient of T_w, c_3, we obtain

$$C_3 \frac{dT_w}{dt} = C_1 + C_2 T_a - T_w + C_4 \cos\left[2\pi\left(\frac{t}{t_y} - c_5\right)\right], \qquad (8)$$

where $C_3 = 1/c_3$, and $C_n = c_n/c_3$ ($n = 1, 2, 4$). If C_3, which is the time scale for adaptation of ST to local conditions, is small enough, then the left hand term will stand for instantaneous adaptation, hence explicitly providing the equilibrium temperature (Toffolon and Piccolroaz, 2015): $T_{w,eq} = C_1 + C_2 T_a + C_4 cos\left[2\pi\left(t/t_y - c_5\right)\right]$. Parameters C_2 and C_4 are the measures of sensitivity to air temperature and contribution of unresolved seasonal inflows, respectively.

Differently from other applications of *air2stream* (e.g., Toffolon and Piccolroaz, 2015; Piccolroaz *et al.*, submitted), because of the short ST record (January-December 2014; including missing values where present), here, the parameters of equation (7) were calibrated using the entire dataset without an independent validation.

3.4 Results

3.4.1 Spatial and temporal variation in stream temperature

The stream temperature (ST) ranged between the maximum and minimum daily value of 27.8°C (July) and 0°C (February), respectively, and showed similar temporal patterns at all sites. Spatially, sites differed in overall and daily means, daily maximum and timing (Table III.2; Fig III.2). During the study period, the largest difference in daily mean ST between sites was observed in May (5.1°C; S20 [15.9°C], S2 [10.8°C] on 05/05/2014) followed by August (4.9°C; S20 [20.2°C], S3 [15.3°C] on 28/08/2014). Local maxima of STs were recorded for sites situated at the outlet of lakes, such as S6 and S10, and sites within urban areas, such as S14, S18, S19 and S20. Also, the timing of maximum ST was earlier at these sites than most of the other sites (Table III.2). Differences of -0.8 to 2.9°C were observed in daily mean STs between sites situated after and before urban areas such as S14-S13, S20-S16. Also, the maximum difference in daily mean STs between post- and pre-lake sites (S5-S6; S9-S10; S18-S16) ranged between 1.3°C to 2.9°C during summer and -0.6°C to -1.4°C in winter. In reaches downstream of lakes, such as downstream of S6 and S10, a progressive cooling was observed in summer. However, for sites situated after lakes and within urbanized areas (such as S18 to S20), such a trend was not observed. On the contrary, the ST increased after passing through the lake up till S20.

The entire ~200 km study reach can be segregated into four sub-reaches which are thermally heterogeneous from each other (Fig. III.1; Table III.2). Sub-reach I flows through a mix of forested and agricultural area with interspersed urban areas in some regions; sub-reach II is majorly dominated by agricultural area; sub-reach III flows through mostly semi-forested/agricultural areas; and sub-reach IV is situated within the Berlin city. The site S17 (within sub-reach III) was a bit peculiar, being much cooler than rest of the sites in sub-reach III during April-July and warmer during January. This could be an indication of a probable local influence of groundwater or the logger might have come in close contact with the riverbed. During summer, a downstream cooling trend within sub-reaches II and III (except warming at S14) was very apparent (Fig. III.2). Across sub-reaches as well, the ST increased downstream, with each sub-reach being warmer than its upstream sub-reach. During winter, the ST decreased downstream, with hardly any differences between sub-reaches II and III (Fig. III.2).

This longitudinal variation in mean ST was observed at sub-daily, daily, weekly and monthly scales and could also be found for maximum and minimum temperatures. The daily temperature range (difference between maximum and minimum ST in a day), however, portrayed a different pattern (Fig. SIII.2). For example, sites S6, S14, S15 consistently had one of the highest ranges during February-July, whereas the rest of the sites did not differ much during the day.

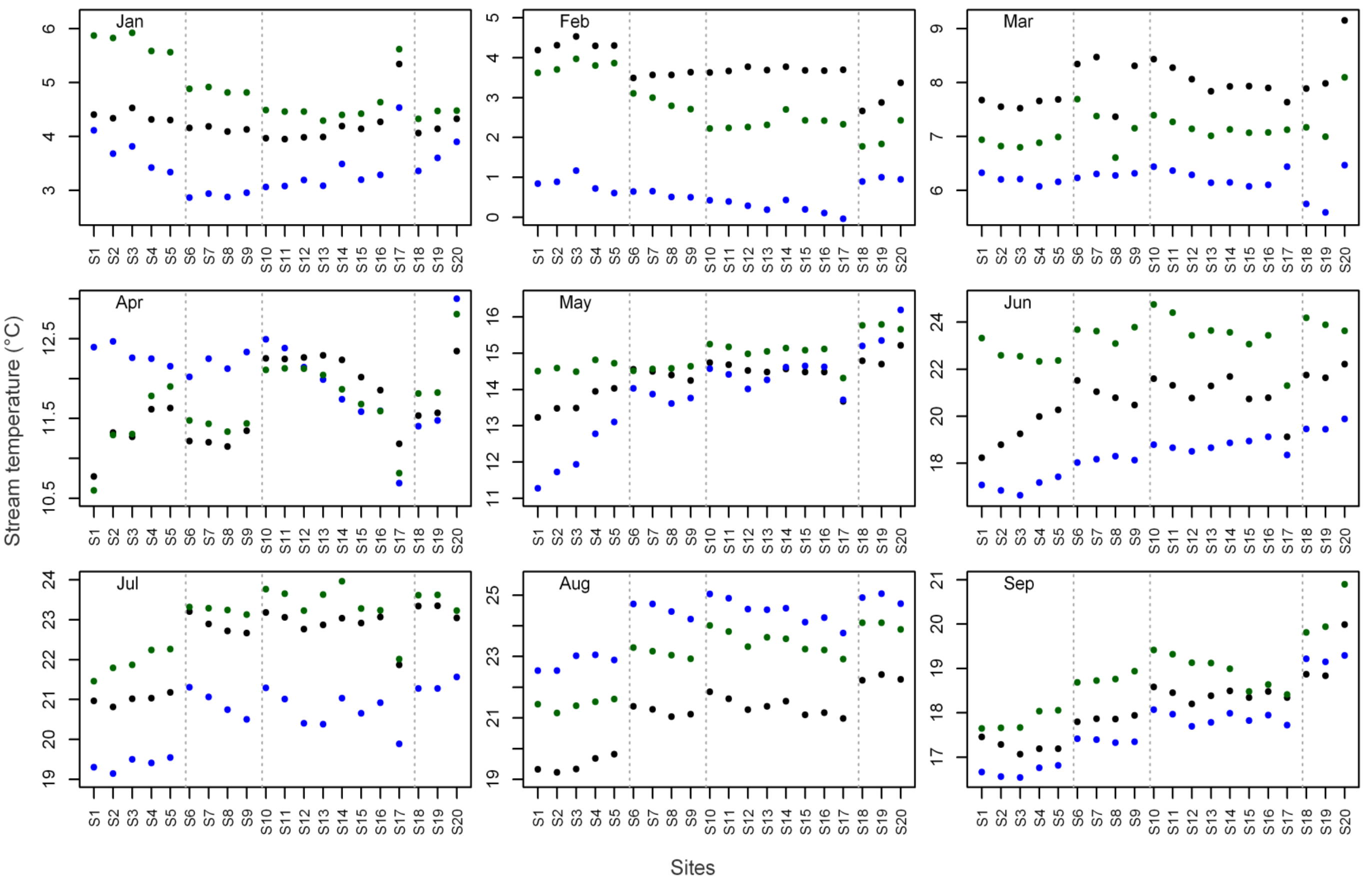

Figure III.2 Daily means for the 4th (blue), 10th (dark green) and 15th (black) day of each month plotted for the 20 sites on River Spree for all months during the study period.

3.4.2 Spatiotemporal variation in the contribution of the 'other' heat fluxes

The residual energy flux term E_r denotes the unresolved contribution of heat flux within a reach via sources other than exchange with the atmosphere, for *e.g.*, due to factors such as land use and inflows from lakes (within the reach), tributaries, groundwater and/or wastewater. The mean E_r for the study period was positive (and highest) for sites at lake outlets and/or within urban areas (namely, S6, S10, S14, S18, S19 and S20), signifying that 'other' sources were a heat source within reaches upstream of these sites (Fig. III.3a). The E_r

term remained positive for up to 52-63% of the entire study period for these sites. At the other sites, either the absence of these inputs or the presence of forested areas caused E_r to be negative, implying cooling. As expected, the major contribution of E_r for reaches with sites S6, S10, S14, S18, S19 and S20 at the downstream end was received during warmer months (June to Sep) (Fig. III.3b, c).

To see how the upstream conditions impact ST behaviour at a site, ST was simulated via the Lagrangian (equation 4) and the "local" Eulerian (equation 5) models for sub-reach II (Fig. III.4). The simulated ST at S9 (downstream site) from the Lagrangian model (mean = 23.5°C, S.E.= 0.023) was very similar to the observed ST (mean = 23.7°C, S.E. = 0.021) at the site during actual conditions while the ST simulated from the "local" Eulerian model was lower (mean = 22°C, S.E.= 0.021) than the observed ST. From this comparison, it appears that the upstream conditions, via advected heat, determine the base ST while the local atmospheric conditions are responsible for deviations from this base temperature. Moreover, through these simulations it could be determined that approximately 70% of total solar radiation was incident on the reach (Fig. III.4a), as the simulated and observed values fit the best at this value. Lowering the amount of incident solar radiation to zero (complete riparian shading) lowered the mean simulated ST (lagrangian) by 1.7°C (Fig. III.4b) and the maximum simulated temperature by 1°C. On the other hand, increasing the incident solar radiation to 100% (Fig. III.4c) increased the mean and maximum simulated temperatures by 0.7°C and 1.1°C, respectively. If the downstream ST was predominantly controlled by local atmospheric conditions, shading would have been more effective in lowering ST (Fig. III.4b, mean = 16.8°C, S.E. = 0.04).

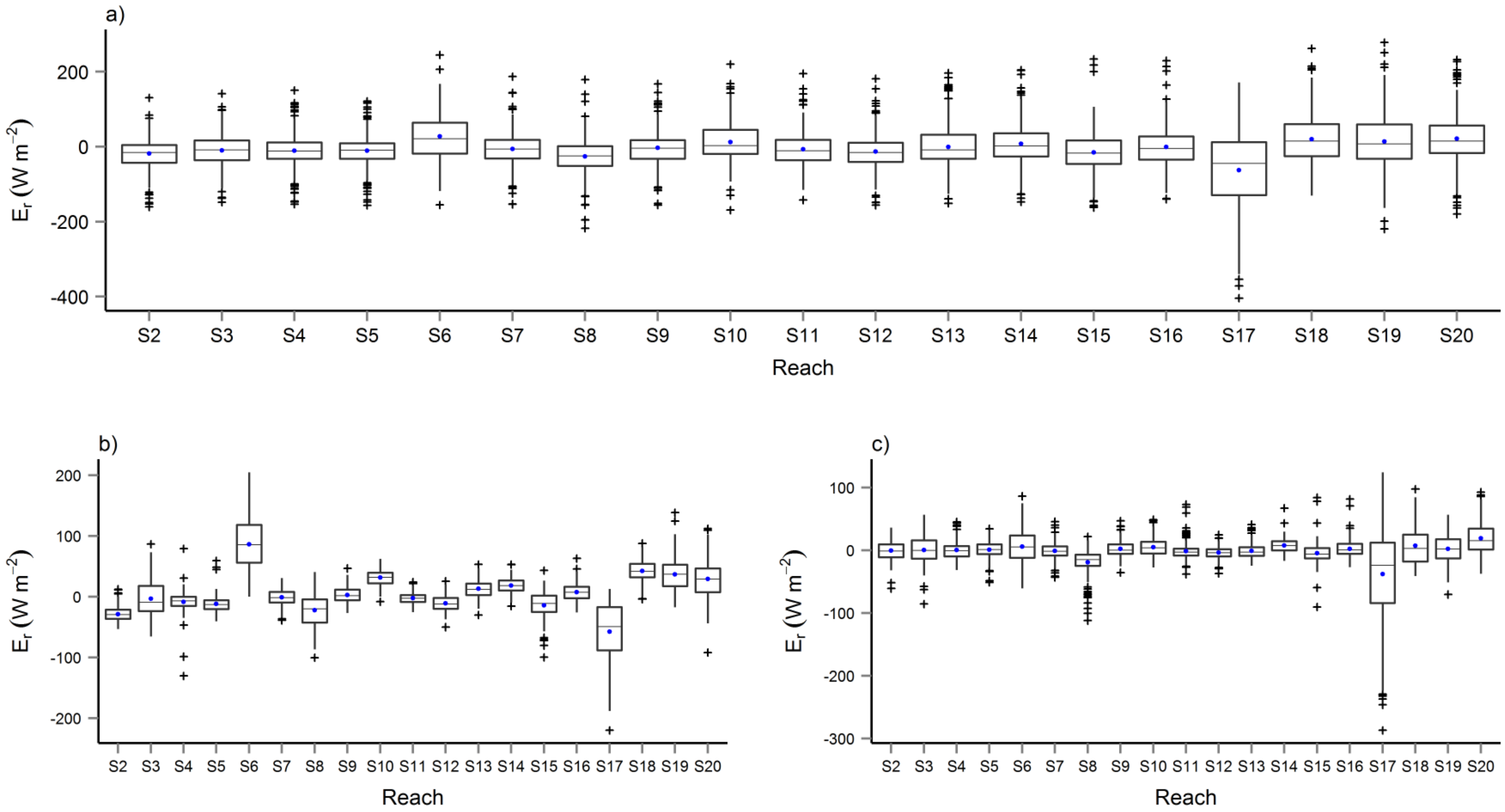

Figure III.3 Boxplots showing E_r values for the entire study period (a), for the warmer months (b; June-Sep) and for the colder months (c; Jan-May) at all reaches on River Spree. Mean values are represented by blue points. Boxes around the median line show the 25th and 75th percentiles with whiskers representing the 5th and 95th percentiles and each cross representing the upper and lower outliers.

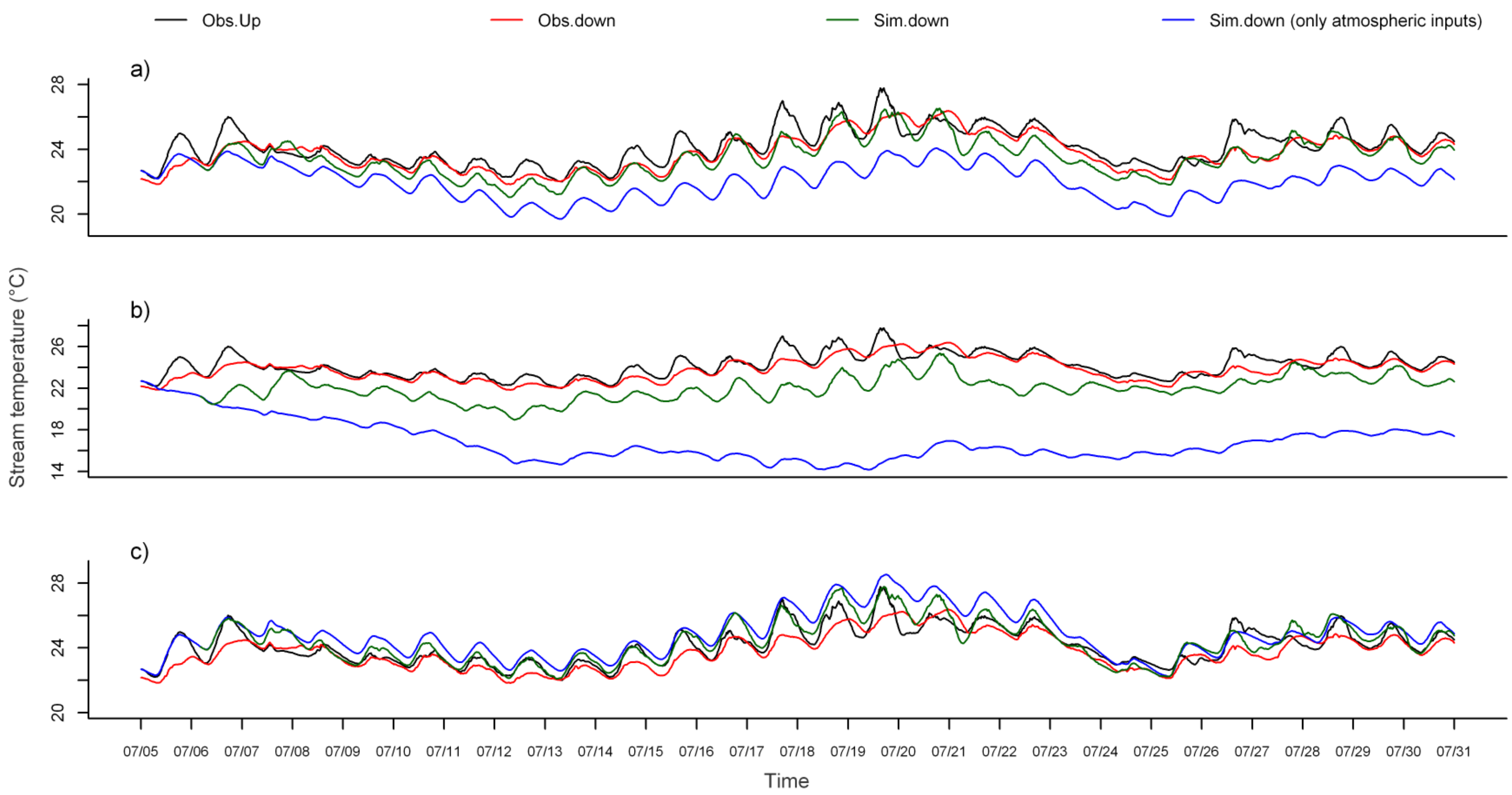

Figure III.4 Simulations of ST at site S9 (downstream) using ST at S6 as input under the Lagrangian (green line) and "local" Eulerian framework (blue line). The simulation was done for three solar radiation conditions: actual (~70%; a), null (0%; b) and all (100%; c).

3.4.3 Dependence on hydro-climatological and landscape variables

3.4.3.1 Correlations with hydro-climatological variables

Among the seven hydro-climatological variables considered, air temperature, solar radiation and relative humidity were fairly linearly related with ST, while the other variables shared a non-linear relationship (Fig. SIII.3, not shown for discharge). Air temperature (82-88%) and solar radiation (54-58%) explained the highest percentage of temporal ST variability for all sites (Fig. III.5). Air temperature contributions decreased consistently from upstream to downstream whereas that of solar radiation remained relatively constant. Discharge, relative humidity and atmospheric pressure explained, on average, 38% (standard error, S.E.= 0.03), 16% (S.E.= 0.001) and 15% (S.E.= 0.002) of ST variability respectively (Fig. III.5). The effect of discharge was the highest for upstream sites S3, S4 and S5, while the lowest was for S2 and S3. Several small forested canals in the lower Spreewald region and the bigger Nordumfluter canal flow into the main stem between S2 and S3 and probably contribute to a larger portion of discharge. Hence, the ST in this reach is largely a reflection of the water temperatures in the canals. Other climatological variables contributed less significantly, explaining < 10% of temporal ST variability. Together, the hydro-climatological variables explained 89-92% (multiple regression) of the ST variability.

Table III.3 Correlations of parameter C4 (*air2stream*), mean stream temperature (for the entire period), mean E_r(for the entire period) with landscape variables (LV). NS stands for not significant correlations.

LV	C4	ST	E_r
F_50	-0.55 (0.016)	-0.52 (0.02)	NS
F_100	-0.54 (0.018)	-0.49 (0.03)	NS
F_500	-0.47 (0.044)	NS	NS
F_1000	-0.47 (0.040)	NS	NS
A_50	NS	NS	NS
A_100	NS	NS	NS
A_500	-0.56 (0.013)	NS	NS
A_1000	-0.61 (0.006)	NS	NS
U_50	0.65 (0.003)	NS	0.47 (0.04)
U_100	0.69 (0.001)	0.49 (0.03)	0.49 (0.04)
U_500	0.72 (0.001)	0.52 (0.02)	0.50 (0.03)
U_1000	0.67 (0.002)	0.47 (0.04)	0.47 (0.04)
Lake distance	-0.48 (0.031)	-0.74 (<0.01)	NS

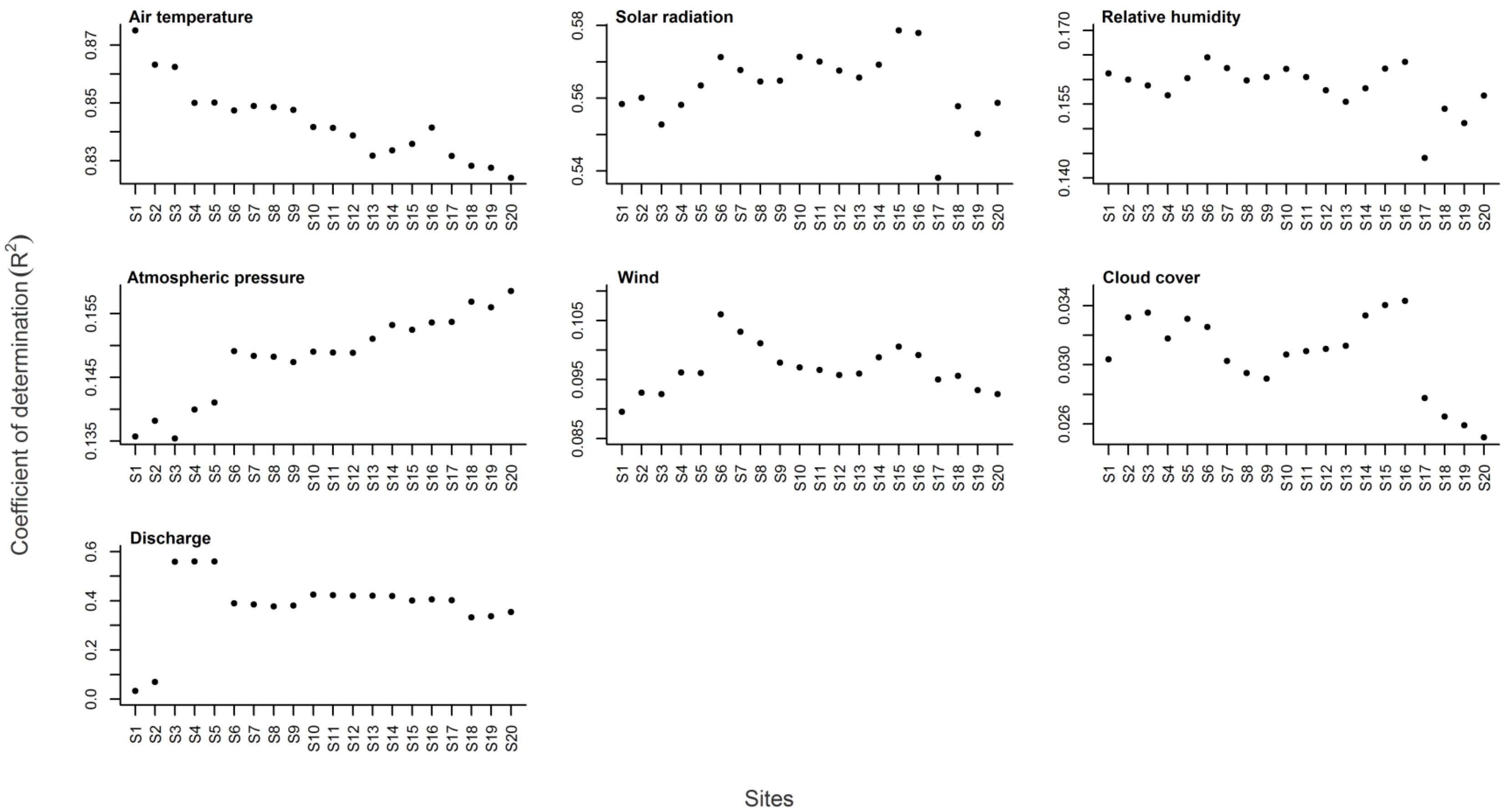

Figure III.5 Values of coefficient of determination (R^2) from linear regression (for air temperature, relative humidity) and non-linear models (for solar radiation, atmospheric pressure, wind, cloud cover, discharge) between daily mean hydro-climatological variables and ST for all sites on River Spree.

3.4.3.2 Correlations with landscape variables

Stream temperature: Several significant correlations of ST metrics with landscape variables were detected at monthly, daily scales as well as for the entire time period. Over the study period, share (%) of urban and forest area in >50 m and ≤100 m wide buffers, respectively, were significantly correlated with the mean STs (Table III.3). At the monthly scale, significant correlations of land use shares with mean STs were observed mostly for warmer months (May-Sep) (Table III.4). Share of forest area within 100 m had a significant negative correlation with both mean and maximum monthly STs. On the other hand, share of urban area showed strong significant correlations with mean monthly STs during warm months (positive) and with maximum monthly STs during February (negative), irrespective of the buffer width (Table III.4). Share of agricultural area was also significantly correlated with mean monthly STs during warm months (≥500 m) and with maximum monthly STs during February (all buffer widths). At the daily scale, share of forest cover within 50 m and urban cover within 500 m had the highest number of significant correlations with mean ST (44% of 259 days) as well as with maximum ST (forest (50 m): 38%; urban (500 m): 36%).

Distance from lakes had a significant negative correlation with the mean ST for the study period (Table III.3). At the monthly scale, mean and maximum STs of warmer months had a significant negative correlation with lake distance, while a significant positive relationship was observed during the coldest months (Table III.4). At the daily scale, significant correlations of lake distance with mean and maximum STs were similar in number (mean = 73.7%; max = 72.2%). No significant correlations between stream azimuth and ST were detected at any time scale.

Residual heat flux E_r: Mean E_r for the study period was significantly correlated with only the share of urban area irrespective of the buffer widths (Table III.3). At the monthly scale, significant correlations of land use cover with mean E_r were also detected mostly for warmer months (Table III.5). Share of forest cover in ≥500 m buffer widths were negatively correlated with mean monthly E_r while urban cover had significant positive correlations for all buffer widths. There were no significant correlations with agricultural cover.

Significant correlations of lake distance with mean monthly E_r were observed, but not with the mean for the entire study period (Tables III.3, III.5). Lake distance had significant correlations with mean monthly E_r in February (positive) and in warmer months (June-Sep; negative correlation). There were no significant correlations with stream azimuth.

Table III.4 Significant correlations between landscape variables (LV, see Table III.1) and mean (bold), maximum (*italic*) monthly STs for all sites. NS stands for "not significant" correlations. P-values for significant correlations are provided within the brackets.

LV/Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
F_50	NS	NS	NS	NS	NS	**-0.49 (0.03)**	**-0.52 (0.02)** *-0.46(0.047)*	**-0.60 (0.01)** *-0.54(0.02)*	**-0.55 (0.01)** *-0.62(<0.01)*
F_100	NS	NS	NS	NS	NS	NS	**-0.48 (0.04)**	**-0.58 (0.01)** *-0.49(0.03)*	**-0.55 (0.01)** *-0.62(0.01)*
F_500	NS	NS	NS	NS	NS	NS	NS	NS	NS
F_1000	NS	NS	NS	NS	NS	NS	NS	NS	NS
A_50	NS	*0.54 (0.02)*	NS	NS	NS	NS	NS	NS	NS
A_100	NS	*0.56 (0.01)*	NS	NS	NS	NS	NS	NS	NS
A_500	NS	*0.61 (0.01)*	NS	NS	**-0.48 (0.04)**	NS	NS	NS	**-0.51 (0.03)**
A_1000	NS	**0.53 (0.02)** *0.56 (0.01)*	NS	NS	**-0.50 (0.03)**	NS	NS	**-0.53 (0.02)**	**-0.59 (0.01)**
U_50	NS	*-0.58 (0.01)*	NS	NS	NS	NS	NS	**0.47 (0.04)**	**0.58 (0.01)**
U_100	NS	*-0.64 (<0.01)*	NS	NS	**0.47 (0.04)**	NS	NS	**0.52 (0.02)**	**0.63 (0.004)**
U_500	NS	*-0.64 (<0.01)*	NS	NS	**0.49 (0.03)**	NS	NS	**0.56 (0.01)**	**0.66 (0.002)**
U_1000	NS	*-0.64 (<0.01)*	NS	NS	NS	NS	NS	**0.51 (0.02)**	**0.62 (0.004)**
Lake distance	**0.67 (<0.01)** *0.77 (<0.01)*	**0.60 (<0.01)**	NS	**-0.50 (0.03)** *-0.66 (<0.01)*	**-0.69 (<0.01)** *-0.70 (<0.01)*	**-0.80 (<0.01)** *-0.78 (<0.01)*	**-0.83 (<0.01)** *-0.84 (<0.01)*	**-0.71 (<0.01)** *-0.85 (<0.01)*	**-0.62 (<0.01)** *-0.81 (<0.01)*

Table III.5 Significant correlations between landscape variables (LV, see Table III.1) and mean monthly E_r for all sites. NS stands for "not significant" correlations. P-values for significant correlations are provided within the brackets.

LV/Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
F_50	NS	NS	NS	NS	NS	NS	NS	NS	NS
F_100	NS	NS	NS	NS	NS	NS	NS	NS	NS
F_500	NS	NS	NS	NS	NS	NS	NS	-0.53 (0.02)	-0.51 (0.02)
F_1000	NS	NS	NS	NS	NS	NS	NS	-0.51 (0.02)	-0.51 (0.03)
A_50	NS	NS	NS	NS	NS	NS	NS	NS	NS
A_100	NS	NS	NS	NS	NS	NS	NS	NS	NS
A_500	NS	NS	NS	NS	NS	NS	NS	NS	NS
A_1000	NS	NS	NS	NS	NS	NS	NS	NS	NS
U_50	NS	NS	NS	NS	NS	NS	NS	0.53 (0.02)	0.50 (0.03)
U_100	NS	NS	NS	NS	NS	NS	NS	0.56 (0.01)	0.55 (0.02)
U_500	NS	NS	NS	NS	NS	NS	NS	0.61 (0.01)	0.60 (0.01)
U_1000	NS	NS	NS	NS	NS	NS	NS	0.57 (0.01)	0.55 (0.01)
Lake distance	NS	0.54 (0.02)	NS	NS	NS	-0.47 (0.04)	-0.49 (0.03)	-0.57 (0.01)	-0.46 (0.05)
C4	NS	NS	NS	NS	0.50 (0.03)	NS	NS	0.67 (<0.01)	0.77 (<0.01)

3.4.4 Evaluation of the semi-empirical model versus regression models with air temperature as input

3.4.4.1 Regression models

The overall performances of the regression models are in general not satisfactory. Linear regression models showed a poor performance with the root mean square error (RMSE) varying from 2.4°C to 3.3°C, with a general tendency of worsening downstream (Fig. III.6). Logistic models fared better than the linear models, given the non-linear (s-shaped) relationship of air temperature with ST. The performance of logistic regression model also worsened downstream, with the RMSE increasing from 1.6°C to 2.4°C (Fig. III.6).

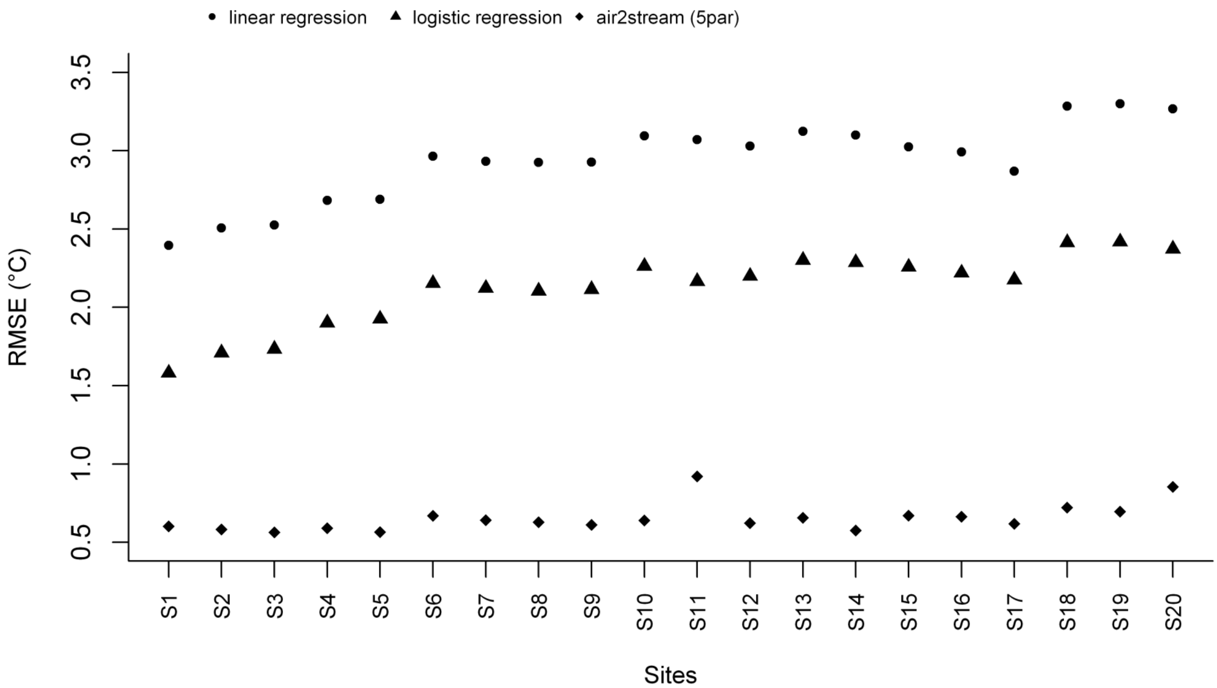

Figure III.6 Root Mean Square Errors (RMSE) for the three models for all sites on River Spree.

3.4.4.2 Semi-empirical hybrid model

Compared to the regression models, the *air2stream* model performed significantly better (RMSE=0.6 – 0.9°C, Fig. III.6; Kruskal-Wallis test, P<0.001). Similar to regression models, the RMSE showed a slight increasing trend in the downstream direction of the reach. Being a hybrid model, the parameters of *air2stream* can be analysed to better understand the dynamics governing the thermal response of the river. The parameter c_3 in equation (7) represents the inverse of the temporal scale of the thermal response to external forcing (Toffolon and Piccolroaz, 2015). The values of this time scale ($C_3 = c_3^{-1}$), which ranged from 2.3 (S1) to 6.7 days (S18), increased from upstream to downstream till S18 and then decreased for the last two sites (Fig. III.7). This suggests that the thermal inertia of the reach increases downstream, implying a greater effect of upstream conditions, thereby increasing the theoretical time taken to reach equilibrium with the local air temperature.

Although the equilibrium version of the model cannot be used because of the relatively long adaptation time C_3, the ratios defined in equation (8) are calculated because they allow for a simpler interpretation than the coefficient of equation (7). Their spatial variation is shown in Fig. III.7. The parameter C_4, which represents the approximate contribution of factors different from air temperature (such as land-use, lake or tributary inputs) to ST dynamics, varied between 2.3 to 5°C. The largest values were estimated for the last three sites in the study reach (S18-S20, Fig. III.7), suggesting that the contribution of the unresolved fluxes was the highest in the city. Parameter C_4 had strong significant correlations with all the land-use variables (Table III.3), except share of agricultural area in ≤100 m buffers. It was positively correlated with the share of urban cover, whereas negatively correlated with agricultural cover, forest cover and lake distance. The overall mean heat flux E_r was positively related with parameter C_4 (significant; r = 0.57; P = 0.01), confirming that both terms quantify the contribution of ‘other’ sources to ST. On a monthly basis, E_r and C_4 had strong and significant positive correlations for the warmer months (May, Aug, Sep) (Table III.5). The parameter C_1, which incorporates the annual constant flux in the model, varied between 3 to 6.2°C, being the highest again for the last three sites (S18-S20, Fig. III.7). The parameter C_2, the coefficient associated with air temperature, varied less than the other parameters (0.6 to 0.8) and was the lowest for site S20 (Fig. III.7).

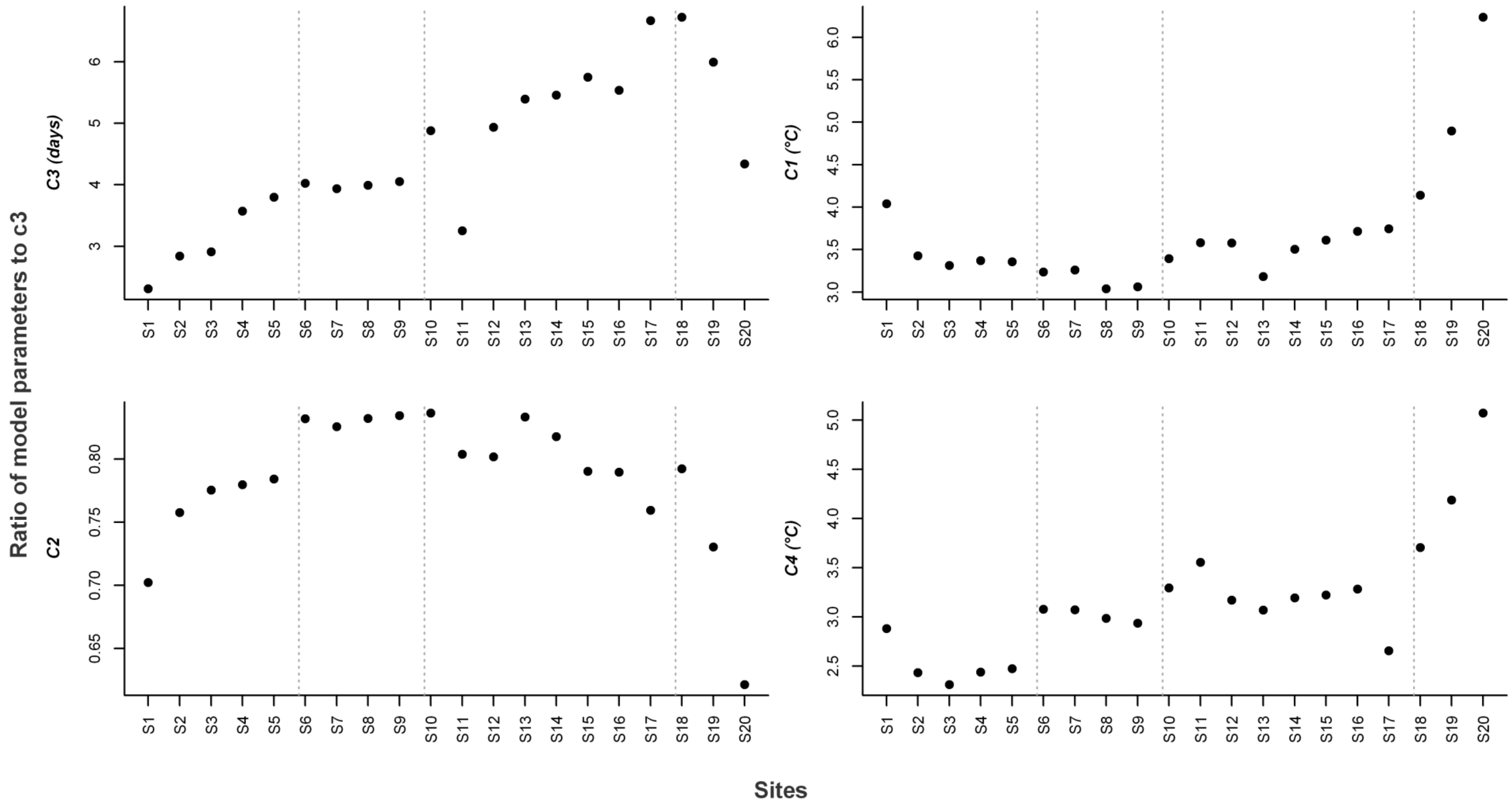

Figure III.7 Spatial variation of the *air2stream* parameters across the study reach. Plots show the ratios of the main model parameters to c_3 (C_1, C_2, C_3, C_4; see equation 8).

3.5 Discussion

3.5.1 Longitudinal heterogeneity in ST and its quantification in the heat budget

Along the 200 km reach, the ST showed similar temporal patterns over the study period at all sites in general. The inter-site differences mainly lay in the timing of daily maximum ST and the magnitude of mean and maximum ST, which were present at almost all time scales. In general, the STs warmed from upstream to downstream in summer, whereas cooled in this direction in winter. Although ST is generally observed to increase with increasing river order (i.e. downstream) (Caissie, 2006), here it is also probable that this was due to the presence of a large reservoir above the study reach, which provided a water temperature that was lower than the equilibrium water temperature in the river.

Based on the observed daily mean ST, the entire reach segregated in four thermally different sub-reaches in warmer months and three sub-reaches in colder months. Presence of lakes and/or presence of urbanized areas rather than the presence/absence of forested areas marked these distinctions. The influence of forested areas on ST is generally known to be more pronounced in smaller streams than in larger streams, where increased stream width prevents complete stream shading and reduces the impact of riparian forest microclimates on the stream energy budget (Hannah *et al.*, 2008; Hrachowitz *et al.* 2010). Passage of river water through lakes and urban areas altered ST, mostly during warmer months, as signified by the larger and mostly positive residual heat flux term, E_r, during summer for reaches containing lakes or cities. During winter, E_r values were quite similar across sites, inferring no significant influence of land use or lakes. Presence of urban areas resulted in ST differences of up to 3°C. Cities tend to create urban heat islands, as air and ground temperature within cities tend to be higher than the rural surroundings (Pickett *et al.*, 2001). Rivers flowing through such heat islands, therefore, also tend to be warmer than rural and forested (Somers *et al.*, 2013). Several other studies have reported similar or larger differences (up to 8°C) between urban and non-urban areas (Pluhowski, 1970; Somers *et al.*, 2013; Booth *et al.* 2014). Pre- and post-lake STs also differed by -1 to 3°C in the examined cases, an observation also made in other studies (Pedersen and Sand-Jensen, 2007; Booth *et al.*, 2014). Mostly, a progressive cooling was observed in sub-reaches downstream of larger lakes in summer, while temperatures remained similar in colder months. Lentic structures such as lakes, ponds and wetlands have been seen to cause a delayed response in ST, resulting in downstream cooling (late summer) and warming (spring) over considerable distances (>100 m) (Mellina *et* *al.*, 2002; Moore *et al.*, 2005; Booth *et al.*, 2014). On the contrary, passage of lake outflows through urban areas showed warming (in summer) as additional heat inputs from urban areas into the river or a higher equilibrium temperature in that region might have prevented heat loss from the reach.

3.5.2 Role of hydro-climatological and landscape variables in inducing longitudinal ST heterogeneity

3.5.2.1 Hydro-climatological variables

Although the temporal variability of STs was largely explained by the usual hydro-climatological variables (such as air temperature, solar radiation, discharge), the contributions of these variables (especially air temperature) decreased downstream of the reach, implying increasing contribution of upstream conditions and/or other sources. Results from the application of the *air2stream* and Lagrangian models corroborated this observation. Lagrangian simulations suggest that the upstream conditions determined the base ST in the study reach, while the climatic variability caused deviations around the base ST. Also, parameter C_4 from the *air2stream* model, which defines the sensitivity of ST to 'other' sources such as landscape variables, showed a general increasing trend, being the highest within urban areas or for sub- reaches with lake inputs.

Values of sensitivity of ST to air temperature (described by the ratio C_2 ≥0.6; Fig. III.7), in the reach was typical of that of large rivers (stream order ≥ 4) (Kelleher *et al.*, 2012). In general, it is expected that ST sensitivity to air temperatures would increase with increasing distance downstream, as it is a function of river size and, hence, of the heat accumulated through the system (Kelleher *et al.*, 2012). However, this trend was seen only in the first 40 km of the study reach, after which the sensitivity either remained constant or decreased, again implying the role of other sources. Both local controls, such as site characteristics, and non-local controls, such as cumulative influence of the upstream network, quantify the magnitude of sensitivity. The sensitivity was the highest for sites situated immediately downstream of lakes (S6, S10). Shallow lakes, such as those found in the study area, present a greater surface area and a longer residence time (as compared to rivers) for receiving solar radiation and sensible heat exchange, thereby more effectively reaching equilibrium with the local atmospheric conditions. Also, water temperatures at lake outlets are probably more influenced by lakeshore water temperatures, which are typically shallower. Sensitivity of ST to air temperature at site S18, which is also below a lake, was not as high as that at the other lake-influenced sites. This is probably because the lake before S18 (lake Müggelsee) is deeper (max. depth = 8 m) than the other lakes (max. depth = 3 m).

3.5.2.2 Landscape variables

Significant correlations with the shares of land cover with spatial ST and E_r variability across sites at different time scales (entire period/monthly/daily) complement the modelling results. The share of urban area (irrespective of the extent; across time scales) and lake distance (mostly at monthly scale) was most consistently related with the spatial variability in ST and E_r. Lower shares of urban cover and greater distance from lakes lead to lower heat inputs during summers and, therefore, lowering ST. These results also suggest that effect of urban areas was not dependent on its proximity to the river, at least when situated within 1 km buffer. In another study, where the local and watershed controls on summer ST were investigated (Booth *et al.*, 2014), local land cover was found to have greater influence on ST while the effect of watershed urbanization was imperceptible. The other important ST controls identified were upstream lakes and watershed geology.

Although forest area did seem to have a significant influence on reducing heat inputs and moderating ST (negatively related to spatial ST and E_r variability during summer), the effective extent buffer width was not clear. With ST, share of forest area within 50 m were significantly related, while with E_r, share of forest area in buffer widths ≥500 m had a significant influence. Hrachowitz *et al.* (2012) also investigated the effectiveness of riparian buffers and attained inconclusive results regarding effective extent, suggesting a dynamic influence of extent of riparian buffers depending on other site-based characteristics such as orientation, discharge, and morphology. Regarding the effectiveness of the longitudinal extent of riparian buffers in lake influenced reaches, presence of complete shading or no shading (up to 20 km) caused a minor change in mean ST and reduced/increased maximum ST by 1°C. This suggests that riparian buffers might not be the best option, or should not be the only one, for regulating ST in the region. Also, the influence of lakes plays a major role in the determining downstream ST and seems to persist over substantial distances.

Spatial variation in land cover variables was related with spatial variability in both daily mean and maximum ST, however, there were more instances of significant correlations with daily mean ST. Although not conclusive, this might suggest a greater influence of land cover on mean rather maximum ST. In contrast, some other studies (Broadmeadow *et al.*, 2011; Imholt *et al.*, 2013) suggest that land cover, such as forest area, influences maximum ST more.

Riparian buffers in the study reach are mostly patchy and, when present, do not shade the river completely, thereby not directly and effectively regulating maximum ST. With respect to urban areas, generally, one of the major pathways through which they effect maximum ST is via contribution of urban runoff (Booth *et al.*, 2014). Considering that this region is one of the driest areas in Germany, it is probable that contribution of urban runoff to maximum ST is not frequent and the average temperatures are being affected via other pathways, consistently occurring on a daily basis.

3.5.3 Beyond regression models

The weak performance of the regression models, especially linear regression, at the daily scale, raises a question regarding their widespread applicability. Generally, air and stream temperature correlations are typically weak at a daily time scale and linear regressions are only accurate at moderate air temperatures (0 to 20°C) (Mohseni and Stefan, 1999; Erickson and Stefan, 2000). However, certain other applications of regression models at weekly scales yielded similar performances (Morrill *et al.*, 2005; Arismendi *et al.*, 2014). Autocorrelation in regression models (first order or second order) weaken their predictive ability, leading to under- or over estimation of values. Autocorrelations are seldom acknowledged by studies and accounting for them could improve the performance of these models (Johnson *et al.*, 2014). Semi-empirical models, such as the one applied in this study, perform with much better accuracy with the same amount of input data and are not affected by problems such as autocorrelation. Moreover, these models were also able to capture and highlight the important reach scale ST controls in the area. Other applications of this model on a wider scale have also revealed similar results (Piccolroaz *et al.*, submitted). As rightly pointed by Arismendi *et al.*, (2014), while the application of simple regression approaches can be attractive, there is a need to move beyond these regression approaches (Toffolon and Piccolroaz, 2015). Modelling approaches, such as demonstrated in this study, provide a wide scope to do so and encourage development of similar or better tools for characterising and predicting ST.

3.6 Conclusion

While between-systems thermal heterogeneity due to landscape variables has been extensively studied, within-system heterogeneity is relatively unexplored and still presents an ongoing challenge (Webb *et al.*, 2008). This study explored the thermal heterogeneity within a 200 km reach of a sixth-order lowland river in Germany (River Spree) and the role of landscape variables such as land use and the presence of lakes. We found that, although the spatial arrangement of land cover classes (forest, agriculture, urban) did not define the thermal regime in the river, the position of urban areas (cities) and lakes were responsible for inducing spatial heterogeneity in the reach. The effect of these landscape variables was similar across various time scales. The influence of urban microclimate on ST was independent of the distance of the urban area from the river edge while the effective lateral extent of forest area was unclear. Hence, rivers flowing through urban landscapes or the rivers with 'urban stream syndrome' need greater attention, while preserving relatively undisturbed upstream sections of such rivers at the same time, as climate change is expected to further alter river thermal regimes in the future. Even though planting or preserving riparian buffers is the most popular management measure to reduce nutrient emissions and to maintain stream temperature, its effectiveness on stream temperatures depends on the morphological and landscape properties of the river. In rivers such as the one studied here, plantation of riparian trees along with other management options such as improving the groundwater table and recharge, managing the temperature of urban discharges or creating shaded artificial ponds might be more effective. Regarding modelling and predicting ST, application of alternative models to statistical regression models at finer time scales is encouraged.

Acknowledgements

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4. Interactions between effects of experimentally altered water temperature, flow and dissolved oxygen levels on aquatic invertebrates

Roshni Arora, Martin T. Pusch and Markus Venohr

4.1 Abstract

River ecosystems are most susceptible to global warming, as temperature rise will often additionally affect regional hydrology and water quality. Hence, in many rivers a combination of rising water temperatures, reduced minimum seasonal flows and changes in the metabolism of matter in river ecosystems is expected. These changes act as multiple stressors on riverine biota, which interact in complex ways and thus may threaten the survival of river biota in unforeseeable ways. As the impacts of multiple stressors acting simultaneously on river biota are not well known so far, we conducted a series of replicated experiments exposing three lowland river macroinvertebrate species [Odonata (*Calopteryx splendens*), Trichoptera (*Hydropsyche pellucidula*), Amphipoda (*Dikerogammarus haemobaphes*)] to a number of combinations (n = 27) of potentially stressful levels of water temperature, flow and dissolved oxygen. Studied species differed in their short-term behavioural responses to stressful conditions, such as drift or inactivity, which were hence chosen to indicate stress. Main effects of water temperature and flow were significant for two out of three species for paired stressor combinations, whereas the low dissolved oxygen levels applied only produced a significant response when combined with other stressors. Significant interaction between variables was detected for temperature and dissolved oxygen for one species (*Dikerogammarus haemobaphes*), with low dissolved oxygen amplifying the negative impacts of high water temperature. These results indicate that the effects of short-term increases in water temperature will affect benthic invertebrates more severely if accompanied by concomitant low dissolved oxygen and flow levels, while interactions among variables obviously vary much among taxa.

4.2 Introduction

River ecosystems are among the ecosystem types most vulnerable to global warming (Woodward *et al.,* 2010a; Isaak and Rieman, 2013). Fluctuations of climate directly affect not only the thermal regime but additionally the hydrological regime of river systems (Arnell and Gosling 2013; van Vliet *et al.,* 2013). Significant rise in water temperature has been reported for several rivers in the past decades (Webb and Nobilis, 2007; Kaushal *et al.*, 2010; Isaak *et al.,* 2012, Orr *et al.*, 2014, Chapter 2), which was often paralleled by changes in flow regimes, especially by decreasing flow levels in summer (Stahl *et al.,* 2010). Rising river temperatures and fluctuating flows trigger various cascading effects on a number of physical, chemical and biological processes in river ecosystems which alter additional aspects of habitat quality in rivers, as dissolved oxygen levels and concentrations of dissolved plant nutrients (Pusch and Hoffmann 2000; Whitehead *et al.*, 2009). These multiple impacts of climate change will further interact with the effects of direct anthropogenic stressors which either amplify or mitigate the effects of climate change through synergistic, antagonistic, or complex interactions (Tockner *et al.*, 2010; Woodward *et al.,* 2010a), posing a multi-faceted imminent threat to the persistence of freshwater biodiversity, and may result in significant deterioration of river ecosystem health (Ormerod *et al.,* 2010; Wooster *et al.,* 2012; Floury *et al.,* 2013; Markovic *et al.,* 2014).

Global warming and concomitantly increasing human demand for freshwater resources–may have severe effects on key variables of river ecosystem functioning, such as water temperature, flow/discharge and dissolved oxygen concentration (DO) (Strayer and Dudgeon, 2010; Woodward *et al.*, 2010a). Changes in the thermal regimes of rivers are known to have impacts on physiological properties and composition of freshwater biota, and on key ecosystem processes (e.g. community respiration) as well. River warming has been shown to result in earlier onset of adult insect emergence, increased growth rates, decreases in body size at maturity, altered sex ratios, decreased densities (Hogg and Williams, 1996), increased taxonomic richness (Jacobsen *et al.*, 1997) and shifts in community structure of invertebrates (Daufresne *et al.,* 2004; Durance and Ormerod, 2007; Haidekker and Hering, 2008). Several key ecosystem processes such as primary production, leaf litter processing and community respiration, and consequently dissolved oxygen levels are also affected (Lecerf *et al.,* 2007; Bärlocher *et al.,* 2008).

Changes in flow velocity influence water quality, sedimentation and channel morphology (Neal *et al.*, 2012), thereby affecting habitat diversity, availability and suitability for riverine biota (Dewson *et al.*, 2007a; Brown *et al.*, 2007). Reduction in flows have been observed to change invertebrate densities, decrease species richness, alter drift rates and shift the community structures (Dewson *et al.*, 2007a, 2007b; Graeber *et al.*, 2013). Similarly, low DO levels also affect invertebrate species survival, emergence, density and abundance (Connolly *et al.*, 2004; Graeber *et al.*, 2013). Concomitant changes in more than one of these parameters, hence, will induce synergistic or antagonistic impacts resulting in complex ecological responses. For many rivers, a combination of rising river temperature and decreasing river flow has been projected in the future (van Vliet *et al.*, 2013), while the responses of riverine biota on such concomitant changes are hardly known so far (Woodward *et al.*, 2010a).

Apart from increasing temperatures due to climate change, another important concern is the increase in frequency of extreme hydro-climatic events such as heat waves, droughts, floods, which happen on short time scales. The frequency of warm events has increased between 1951 and 2010 and is likely to increase further in the future (IPCC, 2013). Such events are likely to have profound and complex consequences for aquatic ecosystems (Lake, 2011). In a recent article (Leigh *et al.*, 2014), these concerns relating to effects of extreme events on river biota have been highlighted. The impacts of hydrological extremes have been studied more (Chessman, 2015; Ledger *et al.*, 2013; Woodward *et al.*, 2012) than the ecological effects of heat waves and hot days on rivers. Responses to heat extreme events may include dispersal, locomotion and other behavioural responses and may also be dependent on habitat type and presence of other stressors (Leigh *et al.*, 2014).

Until recently, only a handful of studies have investigated the relative long-term and short term impacts of multiple changing parameters of water quality, as water temperature, flow and DO, on freshwater invertebrate communities (Table IV.1). Long-term warming of rivers was shown to play a more important role in inducing shifts in invertebrate communities towards thermophilic taxa and those tolerant to multiple stressors (Daufresne *et al.*, 2004; Chessman, 2009; Floury *et al.*, 2013) than discharge changes in French and Australian rivers. A recent stream mesocosm experimental study by Piggott *et al.* (2015) investigated multiple effects of water temperature, nutrients and sediment on community composition and body size structure of benthic, drift and insect emergence assemblages (39 response variables). They showed raised water temperature to be the second most impacting variable (after sediment) and resulted in mainly negative effects on abundance and drift body size. On the other hand, some studies (Durance and Ormerod, 2009; Vaughan and Ormerod, 2014) showed that variations in water quality (including biochemical oxygen demand) and flow explained the trends in abundance and richness of invertebrate species better than water temperature over a period of 18 years. Burgmer *et al.*, (2007) found a significant correlation between changes in macroinvertebrate species composition and shifts in mean temperature observed over two decades in Swedish freshwaters. However, they detected no direct linear effects of water temperature on species composition and diversity. Other local factors such as pH, nutrients and total organic carbon were more important. In general, water temperature appears to be an important and more frequent dominant variable among other water quality variables significantly affecting macroinvertebrate community-based metrics such as structure, diversity, abundance and composition as well as trait-based metrics such as emergence timing, body size, sex ratios and drift rates.

Surprisingly, none of the mentioned studies have studied and compared the relative impacts of increased water temperature, low flow and low DO levels on invertebrates by combined application of those stressors (Table IV.1). Hence, this study aims to address this gap by experimentally investigating short-term behavioural responses, including drift, of several stream invertebrate species in response to varying levels of flow, water temperature and DO, and to combinations of those factors. The test animals were obtained from River Spree, a sixth-order lowland river in northeast Germany, which has suffered temporarily from massive water abstractions (Pusch and Hoffmann, 2000; Graeber *et al.*, 2013), and which is also sensitive to flow reduction by climate change (Kaltofen *et al.*, 2008; Hölzel *et al.*, 2012). Several rivers in Germany, especially in the north-eastern region, have seen decreasing summer flows (Bormann, 2010) and increasing summer river temperatures (Chapter 2). We exposed test animals to levels of key habitat variables which may occur more frequently in rivers affected by climate change, thus acting as stressors. Thereby, we aimed to answer the following three research questions:

a) What are the behavioural responses of studied invertebrate species to extreme values of those factors?
b) What are the tolerance ranges of studied invertebrates in respect to these variables?
c) How does the tolerance range change if two stressors are applied simultaneously?
d) Which combination of stressors is most relevant to limit the occurrence of those species with climate change?

Table IV.1 Review of recent studies on the relative impacts of water temperature (WT) compared to various water quality variables on freshwater macro-invertebrates.

Stress variables	Response variable	Study Period	Reference	Result summary
WT, sediment, nutrients	20 benthos-specific, 13 drift-specific & 6 emergence-specific response variables	3 weeks	(Piggott *et al.*, 2015)	Sediment, WT and nutrients affected 80%, 67% and 58% of all invertebrate response variables, respectively. High WT resulted in mainly negative effects such as reduced abundance.
WT, flow, BOD, nutrients	Taxa richness and prevalence	20 years	(Vaughan & Ormerod, 2014)	Long term changes in prevalence explained better by BOD and flow. Short terms changes in prevalence correlated better with WT and nutrients.
WT, flow, nitrates, phosphates, chlorophyll-a	Macro-invertebrate assemblages, abundance and community composition	30 years	(Floury *et al.*, 2013)	WT, flow and phosphates had the greatest effects on invertebrate richness; shifts in community composition were clearly related to hydro-climatic factors, especially water warming
WT, flow (thermopeaking; hyropeaking)	Invertebrate drift	4 experimental runs; each for 30 min	(Bruno *et al.*, 2013)	Invertebrates exposed to temperature variations require only a disturbance level threshold and not an exposure time threshold to start drifting; drift was higher when the TP wave was followed by an HP wave
WT, flow, nitrogen, ammonia, BOD , orthophosphate	Trends in invertebrate assemblage composition	18 years	(Durance & Ormerod, 2009)	Changing water quality and discharge affected lotic invertebrates more than recent increase in temperature; apparent relationships between temperature and invertebrate variations were spurious
WT, flow	Trends in prevalence of individual families; thermophily, rheophily	13 years	(Chessman, 2009)	Significant relationships between thermophily and rheophily of families and the estimated strength and direction of long-term trends. Climatic changes (rise in WT and decline in flow) favoured thermophilic and non-rheophilous taxa

WT, hydrology, water chemistry, microhabitats, land use, other human impacts	Invertebrate community composition	1 year	(Haidekker & Hering, 2008)	WT was less important for the macro-invertebrate composition in medium-sized streams than in small streams
Climate change, acidification	composition, abundance and stability of macro-invertebrate assemblages	25 years	(Durance & Ormerod, 2007)	Decrease in abundance and changes in composition with increasing temperatures; acidification overrides climatic effects by simplifying assemblages and reducing richness
WT, NAO, DO, pH, TOC, conductivity, nutrients	Composition, diversity, abundance	10-15 years	(Burgmer *et al.*, 2007)	No direct linear effects of temperature and climate indices on species composition and diversity. pH, nutrients and total organic carbon explained a greater percentage of species variance than WT.
WT, flow	Composition, abundance	20 years	(Daufresne *et al.*, 2004)	Increase in thermophillic invertebrate taxa; significantly correlated with thermal variables
WT, ionic content	Oxygen consumption of Gammarids (pleopod beats)	---	(Wijnhoven *et al.*, 2003)	Wide tolerance to temperature for all gammarid species; *G. tigrinus* survived at higher temperatures in the more ion-rich, polluted waters than the indigenous gammarids; tolerance of *D. villosus*, however, was reduced in ion-poor water
WT, flow, pH, conductivity, velocity, substrate	Richness and diversity	---	(Jacobsen *et al.*, 1997)	The number of insect orders and families increased linearly with maximum stream temperature
WT	total animal densities, biomass, and species composition	3 years	(Hogg & Williams, 1996)	Decreased total animal densities particularly Chironomidae (Diptera); earlier onset of adult insect emergence

4.3 Materials and methods

4.3.1 The set-up

The experiments were conducted in an experimental flume 3.0 m long, 0.80 m wide and 0.60 m deep made of 10 mm thick Perspex panels (Fig IV.1). The flume was divided into three sub-channels, each serving as a replicate. The observational area of each replicate was 0.65 m long, 0.25 m wide and 0.10 m deep. A water pump was attached to one end of the flume which provided adjustable flows during the experiments. A mesh screen was installed at the downstream and upstream ends of each observational area, which prevented the escape of insects, and collected the drifting individuals. Fine sand was glued on the bottom PVC plates to provide a suitable colonization substrate for experimental animals.

Flow velocities were determined for each flow level at two locations (2 cm above the bottom) in each compartment (upstream and downstream ends) using an Acoustic Doppler Velocimeter (ADV; Micro ADV 16 MHz, 10 Hz recording; Sontek, San Diego, CA, U.S.A.). Water temperature was regulated by a thermostat heater attached to an immersion rod. Dissolved oxygen concentrations were experimentally adjusted by bubbling air or nitrogen gas through the water.

4.3.2 Invertebrate samples

Three species of invertebrates were selected for the experiments namely the damselfly Banded Demoiselle *Calopteryx splendens* (Harris, 1782), the ‘demon shrimp’ *Dikerogammarus haemobaphes* (Eichwald, 1841) and the caseless caddisfly *Hydropsyche pellucidula* (Curtis, 1834), based on their abundance, body type and flow preferences. The invertebrates were collected by hand nets from the River Spree. Individuals with similar body size were selected for the experiments and kept in separate aquaria at 20°C.

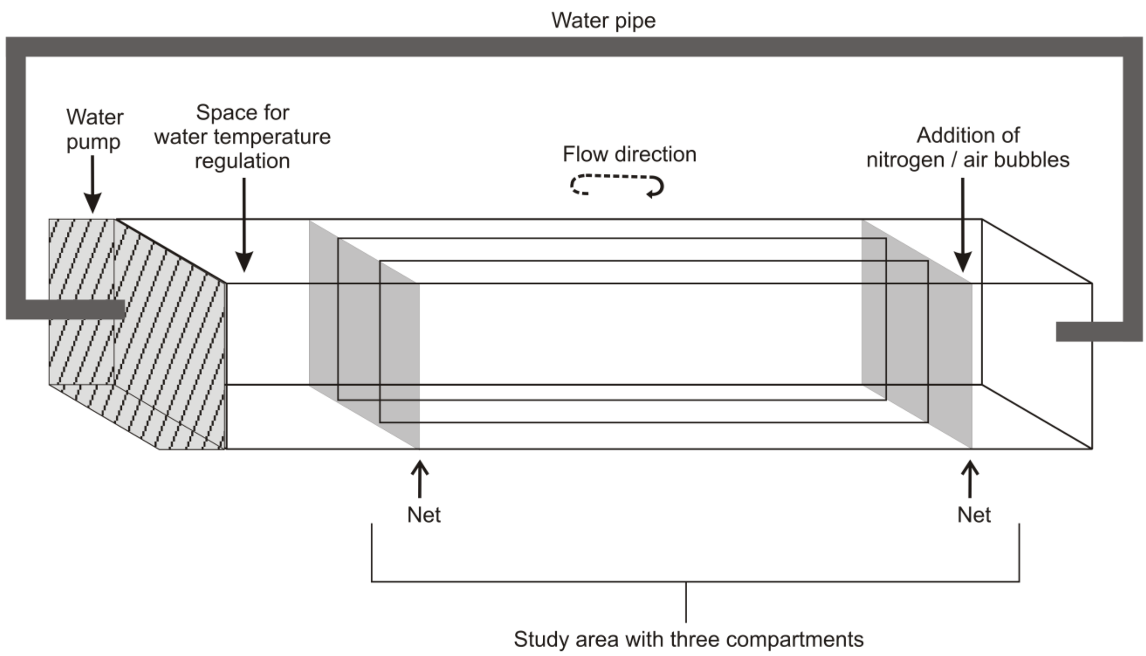

Fig. IV.1 Sketch of the experimental flume

4.3.3 Experimental variables and levels

Three independent variables (water temperature, flow and DO) at three levels (high, medium, low) were used for the experiment (Table IV.2). The chosen upper values of flow and DO and the lower value of water temperature fall very well in the normal ranges found in River Spree. The maximum water temperature recorded in the lower section of River Spree last year was 27.7°C (20 July 2014, 16:00, Alt-Schadow) whereas the daily average flow in the river varied between 2-50 m^3/s (between Fehrow and Sophienwerder; avg.velocity 30 cm/s). In order to mimic a climate change scenario, the highest level of 30°C was chosen for the experiments. At a discharge of 2 m^3/s, the wetted channel of the River Spree is up to 20 m wide and approximately 1 m deep, which results in an average flow velocity of 10 cm/s. Hence, maximum flow in the flume was set to 14 cm/s (with a water depth of 10 cm). The range of daily DO values was 3 to 20 mg/l in the period 2006-2011 for several sites on River Spree (data from the Federal state of Brandenburg, Germany). Low concentrations of DO may especially occur during dawn at low flow conditions with simultaneous high concentrations of planktonic algae or benthic macrophytes, when community respiration is high and physical reaeration is low (Pusch and Hoffmann, 2000). As a threshold value for taxa richness, diversity and abundance metrics for invertebrates was found to be 2.6 mg/l for some lowland streams in North America (Justus *et al.*, 2014), a level of 2.7 mg/l was set as the lowest value for the experiments.

Table IV.2 Experimental levels of the aquatic variables subjected on macro-invertebrate species to determine their responses.

Levels	Temperature (°C)	Flow (cm/s)	Dissolved Oxygen (mg/L)
High	30	14 ± 1	>6.0
Medium	25	11 ± 1	4.0
Low	20	5 ± 0.5	2.7

4.3.4 Experimental runs

The total number of individuals used in the experiments for *C. splendens*, *D. haemobaphes* and *H. pellucidula*, were 27 (9 in each replicate), 30 (10 in each) and 30 (10 in each) respectively, which corresponded to average densities of 49 ind. m^{-2}, 62 ind. m^{-2} and 62 ind. m^{-2}.

In total, we conducted three sub-sets of experiments. Within each subset, two independent variables (two-way interaction) were altered at the three levels for all possible combinations (9 combinations for each sub-set; total runs= 9*3=27). Number of drifting individuals was counted for each run as the response/dependent variable. Each experimental run lasted for 40 minutes, or until when 50% of the population had drifted. Drift observations were recorded every 5 minutes. Between each run, a break of 15-20 min was kept for the animals to de-stress and also to relocate the drifted individuals to their initial locations. Suitable micro-habitats were provided for each species to prevent detachments due to lack of surfaces to hold on to.

An additional sub-set of experiments was conducted for *H. pellucidula* (7 individuals in each replicate), in which ventilatory undulations where also measured as response variable, along with drift. In these set of experiments, two levels of temperature (T1= 25°C, T2= 30°C) and flow (F1= 10 cm/s, F2= 5 cm/s) were chosen and were varied at low DO (≤ 2mg/l). Each run lasted for 30 min.

4.3.5 Data Analysis

Comparisons between drift responses at different combinations of independent variables (Temp-Flow; Flow-DO; Temp-DO) were made using two-way analysis of variance (ANOVA) with the independent variables as fixed factors and drift frequency as dependent variable. Tukey's HSD tests were conducted to detect between-level differences of each independent variable. Deviation of the data from homogeneity of variances and normality (in residuals) was tested using Levene's and Shapiro–Wilk's tests, respectively, before statistical analyses. All statistical analyses were carried out at $\alpha \leq 0.05$ significance level and were performed in R (R ver. 3.2.1; R development core team, Vienna, Austria).

4.4 Results

4.4.1 Behavioural responses to environmental extremes

The three study species showed different behavioural responses in order to cope with limiting levels of water temperature, flow and DO. During low DO-low flow and low DO-high temperature conditions, *C. splendens* individuals seemed to adjust to low oxygen conditions (≤ 2.7 mg/l) by moving closer to the water surface, positioning their gills upwards and/or other movements such as shivering and body pull-downs. They also reduced their drift risk by minimizing their movements and holding on to the substrate. Reduced drift was also observed during most of the high temperature conditions (30°C). *D. haemobaphes* specimens, on the other hand, increased their locomotory activity during stressful conditions such as at high temperature (≥30°C) and low DO levels which increased their probability to drift. During extremely low DO concentrations (<2 mg/l), many individuals moved near the water surface, some even crawling above the surface. *H. pellucidula* responded to stress (such as at high temperature) mostly by drifting and/or by increased ventilatory undulations (especially during low flow-low DO levels).

4.4.2 Experimental Runs

Experiment I: Effect of flow and dissolved oxygen

In the flow and DO experiments series, *C. splendens* and *D. haemobaphes* showed consistent and linear increases in drift with increasing DO level at the highest flow velocity applied (slope > 0, $P < 0.01$) (Fig. IV.2). The pattern may be explained by increasing activity of animals at higher DO levels, which increased their probability to drift. Vice versa, lower drift rates at lower DO levels may be interpreted as suppression of activity due to low DO. *C. splendens* also showed a significant linear response to increasing levels of flow at low and medium DO concentrations ($P < 0.05$) which reflect the increased probability to drift with increasing flow velocities at reduced DO levels. The drift slopes for other combinations of experimental conditions were also significantly different from zero (except at low flow), although the responses were not linear. For *H. pellucidula,* although the drift responses were statistically significant at medium flow velocity and medium DO levels ($P < 0.05$), none of them were linear over the whole observed range. For the other combinations of experimental conditions, no significant consistent response patterns could be detected.

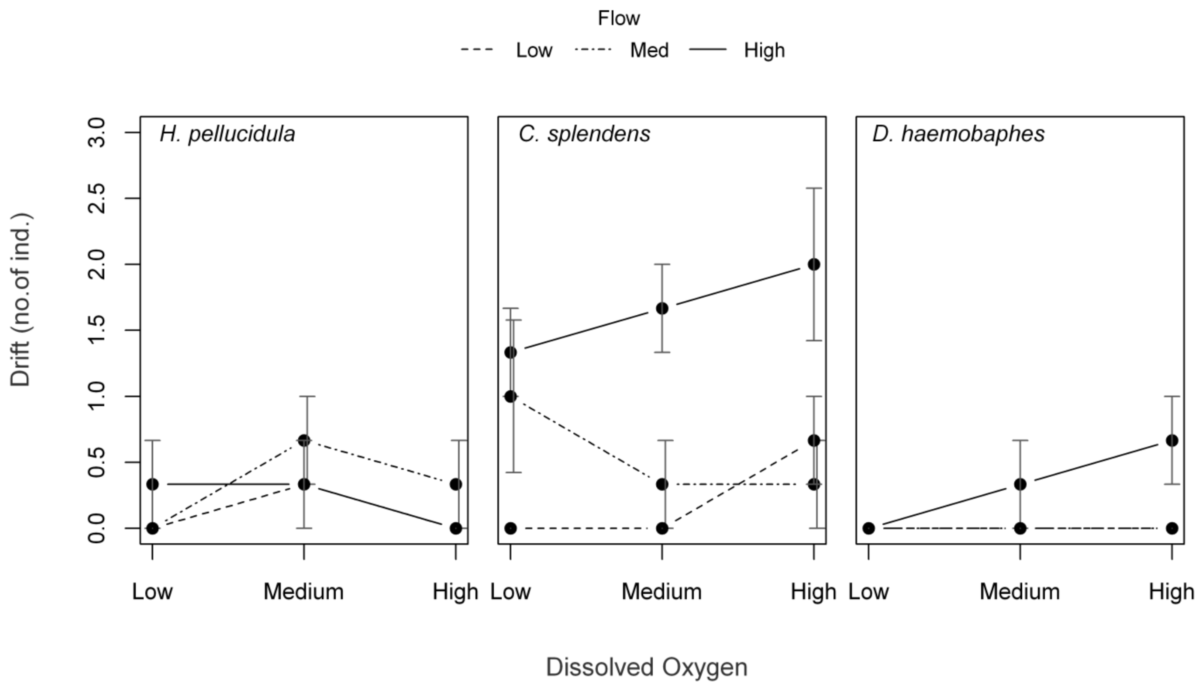

Figure IV.2 Interaction plot of flow and DO for the three study species showing the mean number of detached individuals (average for the three replicates ± SE, n=10 for *D. haemobaphes* and *H.pellucidula*; n=9 for *C. splendens)*

Results from two-way ANOVA revealed a significant main effect of flow for *C. splendens* and *D. haemobaphes* (*C. splendens:* $F(2,18) = 12.6$, $P < 0.001$; *D. haemobaphes:* $F(2,18) = 4.5$, $P = 0.03$) whereas no significant main effect of DO (*C. splendens:* $F(2,18) = 0.6$, $P = 0.5$; *D. haemobaphes:* $F(2,18) = 1.5$, $P = 0.3$) or interaction effect of flow and DO on the drift response (*C. splendens:* $F(4,18) = 1.2$, $P = 0.4$; *D. haemobaphes:* $F(4,18) = 1.5$, $P = 0.2$) could be detected. Between-level comparisons for flow showed that drift responses at low flow and medium flow were significantly different from that at high flow velocity for both *C. splendens* ($P<0.01$) and *D. haemobaphes* ($P = 0.04$). None of the main effects of flow ($F(2,18) = 0.6$, $P = 0.6$) and DO ($F(2,18) = 1.8$, $P = 0.2$) or the interaction effects ($F(4,18) = 0.6$, $P = 0.7$) were significant for *H. pellucidula*.

Experiment II: Effect of water temperature and dissolved oxygen

In the case of varying water temperature and DO levels, *C. splendens* showed a steady and significant increase in drift response with increasing DO levels at low temperature (slope significantly different from zero, $P < 0.01$) (Fig. IV.3). Drift responses to temperature were significant at all DO levels ($P = 0.02$), however a linear decrease with increasing temperature levels was seen only at high DO level. *C. splendens* were seen to have minimized movements and either positioned their setae upwards or shifted closer to the water surface during the high temperature and low DO condition. *D. haemobaphes* showed significant linear decrease with increasing DO levels at high temperature ($P<0.001$), whereas a non-linear increase with increasing temperature levels at low DO level ($P = 0.02$). Significant drift responses were observed for *H. pellucidula* at all DO levels and temperature levels (except at low temperature) ($P< 0.05$). However, the drift increased linearly with increasing DO levels at high temperature and with increasing temperature levels at low and high DO levels (Fig. IV.3).

Overall, water temperature had a significant (*C. splendens:* $F(2,18) = 8.6$, $P = 0.002$; *D. haemobaphes:* $F(2,18) = 12$, $P < 0.001$; *H. pellucidula:* $F(2,18) = 9.1$, $P = 0.002$), and DO had no significant main effect on drift responses for all species (*C. splendens:* $F(2,18) = 0.3$, $P = 0.8$; *D. haemobaphes:* $F(2,18) = 0.4$, $P = 0.7$; *H. pellucidula:* $F(2,18) = 1$, $P = 0.4$). The interaction of temperature and DO had a significant effect only on the drift response of *D. haemobaphes* ($F(4,18) = 3.4$, $P = 0.03$), showing an amplified increase in drift frequency at high temperature and under low DO concentrations, whereas it was subdued under high DO levels.

Among the temperature levels, *C. splendens* drift response at low temperature was significantly different from that at medium and high temperature ($P = 0.005$). For *H. pellucidula*, the drift response at high temperature was significantly different than at low temperature ($P = 0.001$) whereas *D. haemobaphes* drift response at high temperature was significantly different than at both low and medium temperature levels ($P < 0.005$).

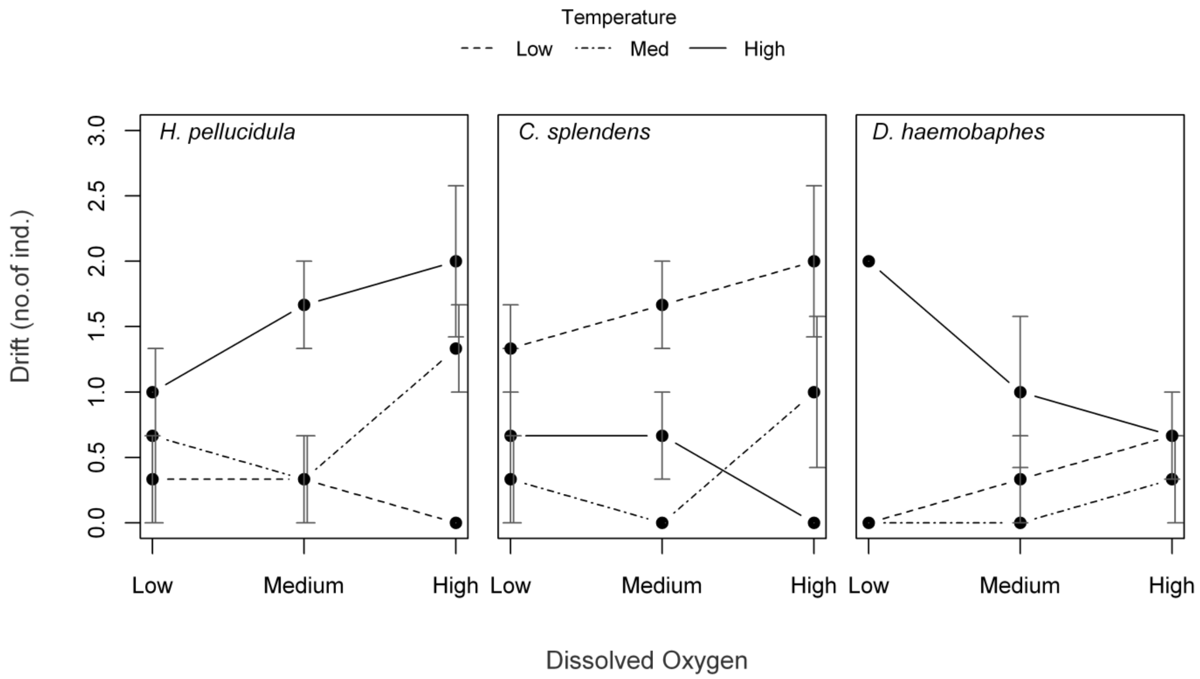

Figure IV.3 Interaction plot of water temperature and DO for the three study species showing the mean number of detached individuals (average for the three replicates ± SE, n=10 for *D. haemobaphes* and *H.pellucidula*; n=9 for *C. splendens)*

Experiment III: Effect of water temperature and flow

For temperature and flow level combinations (Fig. IV.4), *H. pellucidula* showed significant drift responses at all flow levels ($P < 0.05$), with drift frequency linearly increasing with increasing temperature levels. The drift responses to increasing flow at high and medium temperature levels were significantly different from zero ($P < 0.005$) although the responses were not significantly different from each other ($P>0.1$). *C. splendens* drift responses to temperature were significant at high flow conditions ($P < 0.001$) where drift frequency decreased linearly with increasing temperatures. Significant but non-linear drift responses to flow were observed at low ($P < 0.001$) and medium temperature levels ($P = 0.03$). *D. haemobaphes* drift response to temperature was only significant at high flow conditions ($P < 0.001$) and was inactive for most experimental runs. *D. haemobaphes* was very resistant to experimental conditions relative to other species, while *H. pellucidula* exhibited relative high drift.

Among the independent variables, main effect of water temperature on drift response was significant for *C. splendens* ($F(2,18) = 6.1$, $P = 0.01$) and *H. pellucidula* ($F(2,18) = 8.1$, $P = 0.003$) whereas main effect of flow was significant for *C. splendens* ($F(2,18) = 4.3$, $P = 0.03$)

and *D. haemobaphes* ($F(2,18) = 8.3$, $P = 0.003$). Interaction effect of temperature and flow on drift response was not significant for any of the species. Comparison between temperature levels showed that drift response at low temperature was significantly different from high temperature for both *C. splendens* (P = 0.007) and *H. pellucidula* (P = 0.002). Among flow levels, that drift response at high flow velocity was significantly different from drift response at both medium and low flows (P < 0.01) for *D. haemobaphes* whereas for *C. splendens* it differed significantly from the drift response at medium flow (P = 0.04).

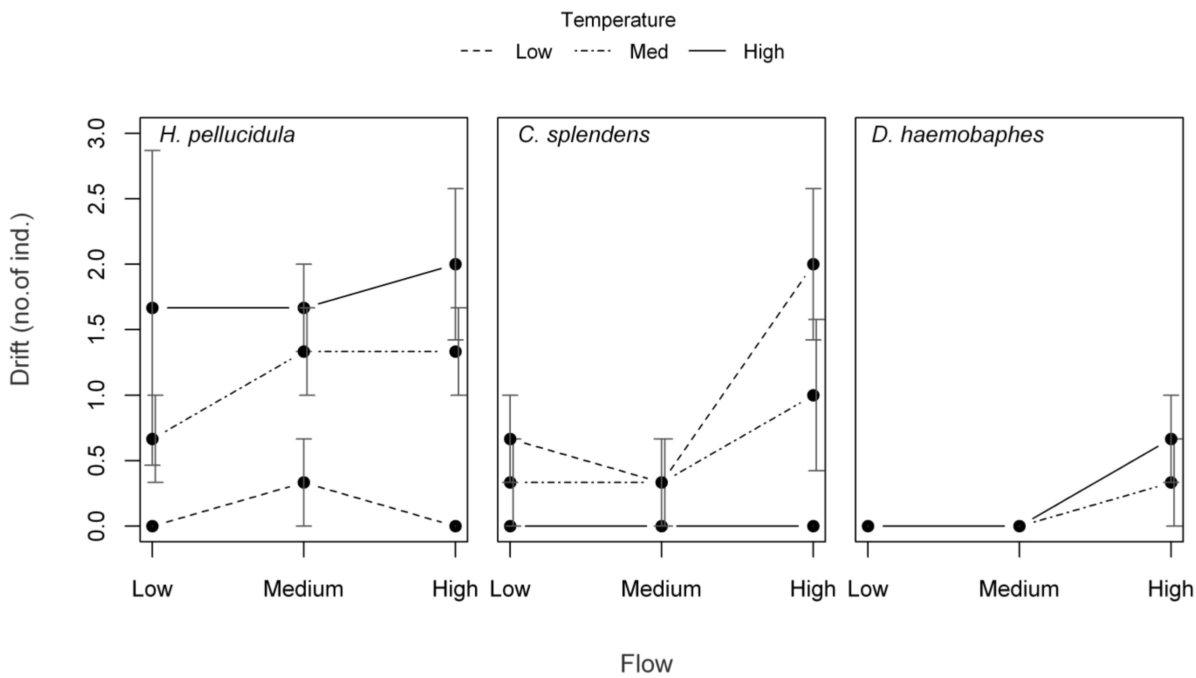

Figure IV.4 Interaction plot of water temperature and flow for the three study species showing the mean number of detached individuals (average for the three replicates ± SE, n=10 for *D. haemobaphes* and *H.pellucidula*; n=9 for *C. splendens*)

Observation of undulation movements in Hydropsyche

Ventilatory undulations in *Hydropsyche sp.* are also an indicator of stress response, with frequency of undulations increasing with increasing stress (Philipson and Moorhouse, 1974). Observation of undulatory movements showed that this behaviour started at the same flow level (5-10 cm/s) as drift response and decreased with increasing flow velocities (Fig. IV.5). The frequencies of both responses were observed to be higher at higher temperature (30°C). Ventilatory undulations were only visible during low flow conditions.

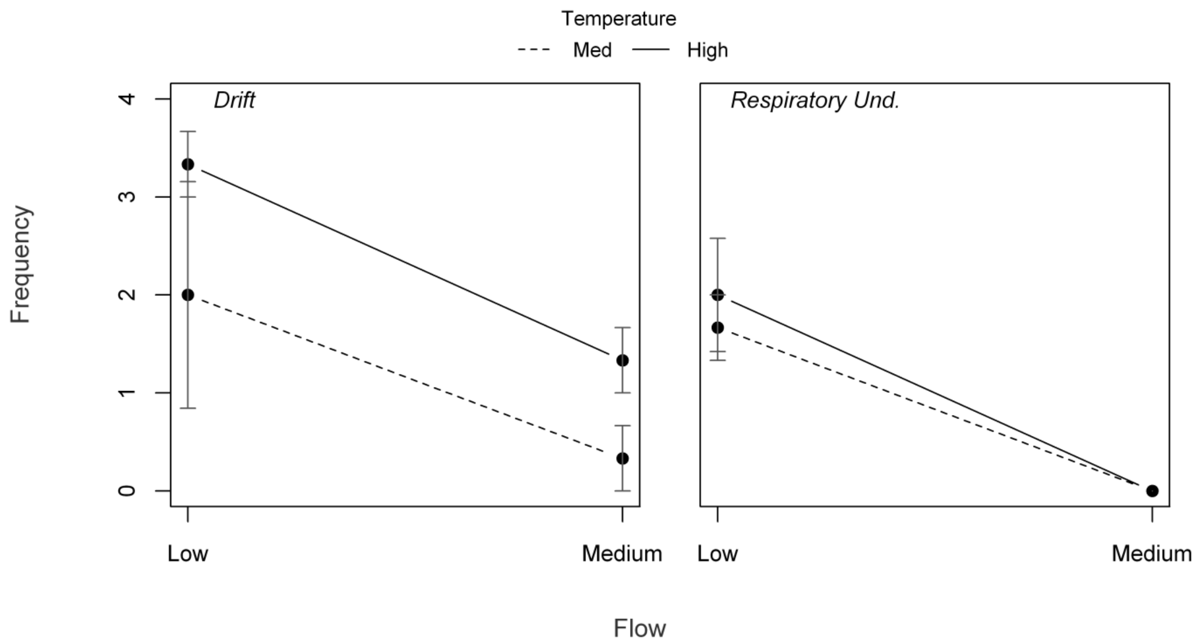

Figure IV.5 Interaction plot of temperature and flow at low DO level (< 2 mg/l) for *H. pellucidula* showing the number of individuals detached and the number of individuals showing respiratory undulations (average for the three replicates ± SE, n=7).

4.5 Discussion

4.5.1 Behavioural responses to multiple environmental stressors

For most organisms, one of the first and most sensitive responses to stress is through changes in behaviour which is a biochemical reaction controlled by neurological and hormonal pathways (Gerhardt 1996; Boyd *et al.*, 2002). Behavioural responses are linked to ecological consequences in a system at every level (Gordon, 2010), be it at the organism (e.g. reduced performance), population (e.g. reproduction success, emergence) or community levels (e.g. predation) (Gerhardt, 1996). Changes in behaviour due to aquatic stress/pollution include increased downstream invertebrate drift, avoidance, changes in gill ventilation, feeding rates and locomotion (Brittain and Eikeland 1988; Gerhardt 1996; Boyd *et al.*, 2002).

In this experiment, the drift frequency of three invertebrate species was measured as a stress response to varying levels of water temperature, flow and DO. Drift is an important mechanism for benthic invertebrate dispersal and colonization and also as an avoidance and escape strategy from life threatening conditions (Townsend and Hildrew, 1976). It affects various aspects of their population dynamics and serves as an important pathway for energy transfer within river systems (Gibbins *et al.*, 2010). During the experiment, we noted that the study species responded differently to stress and not necessarily by drifting. The caseless caddisfly *H. pellucidula* responded to stressful conditions mostly by drifting or by increasing ventilatory undulations. Highest drift frequencies were observed at high water temperature (30°C) regardless of flow and DO levels, whereas the characteristic ventilatory undulations (Phillipson and Moorhouse 1974) were triggered during low flow (≤ 5cm/s) and low DO (< 2.7 mg/l) conditions. These undulations increased with water temperature, a result also observed by Phillipson and Moorhouse (1974). *Hydropsyche sp.* is among the dominant drifting invertebrates (Wetzel, 2001) and has been shown to tolerate temperatures up to 28°C (Sherberger *et al.*, 1977) and low oxygen concentrations below 2 mg/l (Connolly, Crossland and Pearson, 2004, Philipson and Moorhouse, 1974). Since it is a rheophilic species, it can sustain high velocities up to at least 60 cm/s and low flow velocities down to 5±2 cm/s (Philipson and Moorhouse, 1974; Brunke *et al.*, 2001). This could explain why more significant responses where observed for temperature than for other variables.

The damselfly *C. splendens*, on the other hand, showed little activity during stressful conditions. During high temperature (30°C) and reduced flow (5 cm/s) or DO (≤ 2.7 mg/l) levels, *C. splendens* showed little or no drifting due to minimization of movement. An explanation could be that animals tend to reduce their activity and wait at reduced metabolic rates for conditions to improve (Connolly *et al.*, 2004). Other behavioural responses such as vertical migration, shivering, especially during low DO levels, were also observed. Such behaviour provide additional flexibility for the animals to deal with hypoxia (Apodaca and Chapman, 2004). On the contrary, increased movement (locomotion, fighting), and hence drift, was observed during suitable conditions such as during low temperature and high flow/DO levels. Drifting due to loss of foothold during such activities could explain increasing drift rates in favourable conditions (behavioural drift). In general, *Calopteryx sp.* is known to tolerate velocities up to 77 cm/s (Dorier and Vaillant (1953/1954), Schnauder *et al.*, 2010). It is also tolerant to high water temperatures up to 30°C under normal oxygen conditions (Verberk and Calosi, 2012) and can survive low DO levels through behavioural responses (Apodaca and Chapman, 2004; Miller, 1993).

The amphipod crustacean *D. haemobaphes*, in general, showed lack of any activity and spent most time sheltered in the crevices of the flume. During stressful conditions (high temperature and low DO), the individuals showed increased locomotion. It appears that *Dikerogammarus sp.* is relatively inactive species (Gabel *et al.*, 2011; Maazouzi *et al.*, 2011) spending most their time sheltered under stones or other similar substrates. It has been shown to tolerate temperatures up to 27-30°C (Kititsyna, 1980; Wijnhoven *et al.*, 2003; Maazouzi *et al.*, 2011). It requires highly oxygenated waters (Boets *et al.*, 2010) and is comfortable in the velocity range of 8-16 cm/s (Schnauder *et al.*, 2010).

4.5.2 Temperature stress in a multiple stressor context

Alteration of water temperature with flow or DO resulted in significant effects on the study species. During temperature and flow alterations, both temperature and flow had a main significant effect on two out of three species. Lack of any interaction between water temperature and flow indicates that negative impacts of high water temperatures were not offset by increasing flows and vice versa. Water temperature, when varied along with DO, had a significant main effect on all three species whereas DO had no significant effect. Interaction among variables was detected for temperature and DO only in the case of *D. haemobaphes* indicating that negative impacts of high water temperatures were amplified under low DO conditions whereas were offset at high DO levels. Aquatic ectotherms which lack efficient respiration techniques (such as *Dikerogammarus sp.* which require high oxygen levels) are especially vulnerable to the multiple stressor effects of increased water temperatures and reduced levels of oxygen (Verberk and Bilton, 2013). These results demonstrate that water temperature, in the given set of experimental conditions, had a greater effect than any of the other variables in a multiple stressor context. Among coupled variable effects, our results indicate that on a short time scale, concomitant variation of water temperature and flow will have stronger impacts than when temperature and DO or flow and DO are varied together.

Several other experimental studies on water temperature effects corroborate these conclusions. Phillipson & Moorhouse (1974) observed ventilatory and net-spinning activities of three *Hydropsychidae* species under varying water temperature (2-25°C), flow (0-40 cm/s) and DO (1-10 mg/l) levels. From their study, they concluded that although flow will be important in determining the micro-distribution of the species, water temperature is likely to play a more important role in successional and geographical distribution, with DO operating in particular circumstances. Hogg and Williams (1996) conducted a large scale field experiment in which they investigated the effects of thermal manipulation on the total macroinvertebrate densities, biomass, and species composition. They found that small changes in water temperature resulted in measurable responses by the resident invertebrate populations such as reductions in total densities, increased growth rates, earlier emergence, precocious breeding, decreases in body size at maturity, and altered sex ratios. They also observed variable responses of individual species to the manipulation suggesting that responses to changes in temperature are not universal and may be more prevalent within certain groups. Within geothermal streams as well, water temperature of geothermal fluids had a greater influence than the chemical component in determining benthic community features in Big Sulphur Creek, significantly altering benthic community structure and macroinvertebrate density (Lamberti and Resh, 1983). In a more recent study by Piggot *et al.* (2015), experimental simulations showed that among sediment, water temperature and nutrients, water temperature was the second-most impacting variable on macroinvertebrate community dynamics. It affected 67% of the 39 measured response variables including drift EPT richness. Increasing water temperature negatively affected drift EPT richness, drift body size, total abundance, total EPT abundance whereas positively affected community diversity and evenness. Interactive effects of water temperature with nutrients and/or sediments were also significant for several response variables such as total drift propensity and emergence.

Results from some observational studies also support these results. Investigation of water quality factors affecting invertebrate community structure and composition over 30 years revealed that water warming explained a greater percentage of variance irrespective of taxonomic-based metric than discharge (Floury *et al.,* 2013). Durance and Ormerod (2007) also observed significant declines in abundance and changes assemblage composition with increasing temperatures over a 25-year period. Vaughan and Ormerod (2014) found that short-term variations in taxon prevalence correlated primarily with temperature and nutrient concentrations while long-term (21 years) increases or decreases in taxon prevalence correlated better with discharge and pollution sensitivity. Similar results have been also observed for other aquatic biota as well. For example, Wenger *et al.* (2011b) showed that temperature increases themselves played a dominant role over flow in driving future declines of cutthroat trout, brook trout, and rainbow trout fish species. However, some other studies (Burgmer *et al.*, 2007; Durance and Ormerod, 2009; Dohet *et al.*, 2015) reported that water quality, discharge and land-use had larger effects on invertebrate assemblage composition than temperature highlighting that long-term temperature effects become apparent in better water quality conditions. These results also suggest that the time scale over which the multiple stressor effects are studied might influence the group of factors responsible for the ecological responses observed. The lack of interaction effects observed between temperature-flow and flow-DO in our experiment might also be a result of the choice of time scale.

The results of this experiment are particularly relevant when viewed in relation with hydro-climatic extreme events, which occur at short time scales. Our results suggest that when heat wave (high water temperature) is accompanied with drought-like conditions (low flow) for short periods of time, the effect of heat wave might override the low flow effects for certain species (*H. pellucidula*) while low flow effects might dominate or act along with heat wave effects for some other species (*C. splendens*, *D. haemobaphes*). Such impacts of coinciding extreme events might lead to abrupt changes in species compositions and distributions and might affect future responses of the ecosystem to similar events (Leigh *et al.*, 2014).

4.6 Conclusion

Although already several studies have addressed the issue of multiple stressors on river ecosystems, studies specifically looking into multiple effects of water temperature along with other stressors are relatively scarce. Despite the short time scale of the study, several significant results were detected. In general, our experiment showed dominant effects of water temperature over flow and DO and dominant water temperature-flow effects on the behavioural responses of three lowland invertebrate species on short time scales. However, the main and interactive impacts of multiple stressors varied across species depending on their tolerance ranges for water temperature, flow and DO and induced different behavioural responses. We conclude that the effects of human-induced shifts in river water temperature on benthic invertebrates may be modified by concomitant limiting conditions of DO and flow, but that those interactions highly depend on the physiological and behavioural patterns of species, and on the stress level range involved. Available information suggests that interactions of multiple stressors may occur at larger spatial and temporal scales, too, but which needed a much larger design to be demonstrated experimentally.

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5. GENERAL DISCUSSION

5.1 Rationale and research aims

River systems worldwide are threatened as a result of climate change and anthropogenic modifications which impact thermal and hydrological regimes (Ormerod *et al.*, 2010). A significant rise in water temperature has been reported for several rivers in the past decades (Webb and Nobilis, 2007; Kaushal *et al.*, 2010; Isaak *et al.*, 2012, Orr *et al.*, 2014) and this trend is expected to continue in the future (van Vliet *et al.*, 2013). Given the crucial role that river temperature plays in governing several river processes, understanding the dynamics, processes, controls and drivers of change of river thermal regimes is of prime importance. Several previous studies on river temperature have helped gain insight on the primary controls of river temperature behaviour and the direct/indirect impacts of environmental changes on river temperature. However, there is still a need to further improve our understanding of the spatial and temporal heterogeneity in river temperatures (Webb *et al.*, 2008). More precisely, the role of hydro-climatological (such as air temperature, flow) and landscape variables (such as land use, altitude) in causing river temperature heterogeneity over a range of temporal and spatial scales needs to be further clarified. Furthermore, river systems are exposed to an array of stressors, which interact in complex ways to result in either synergistic, antagonistic or no net effects on freshwater biodiversity (Ormerod *et al.*, 2010; Jackson *et al.*, 2015). While a few studies have investigated the long-term impacts of multiple stressors on freshwater biota, studies investigating the short-term impacts of simultaneously changing physical aquatic parameters such as water temperature, flow and dissolved oxygen, on freshwater macroinvertebrates are extremely scarce.

Therefore, this thesis aimed to address these gaps by observing and quantifying river temperature changes over several spatial and temporal scales. In Chapter 2, long-term (25 years) and short-term changes (10 years) in river water temperature were quantified and the roles of climatic, hydrological and landscape variables were identified for German rivers on a regional basis. In Chapter 3, spatial heterogeneity in water temperature of a lowland river reach (~200 km) was observed and quantified via a heat-budget model and a semi-empirical model over a period of nine months. In addition, the role of landscape factors in causing the observed heterogeneity was investigated. Furthermore, the efficacy of riparian shading in moderating river temperature downstream of lakes was tested. In Chapter 4, the behavioural response (namely drift) of three river macroinvertebrate species to varying levels of water temperature, flow, and dissolved oxygen, and to combinations of these factors were experimentally investigated to characterize the relative influence of rising water temperature in a multiple-stressor context.

5.2 Key research findings

The novelty of the research presented in this thesis lies in: (a) conducting the first assessment of long-term and short-term changes in river temperature for Germany and identifying the contribution of air temperature changes, flow changes, changes in climatic phenomena (such as the North Atlantic Oscillation) and landscape variables (such as altitude, catchment area, ecoregion, land use), in the observed changes in river temperature; (b) assessing the influence of the presence and lateral extent of different types of land use (such as forested, agricultural and urban areas) and other landscape features (such as lakes) in inducing reach-scale thermal heterogeneity and quantifying the observed heterogeneity using a simple heat budget and a semi-empirical model; (c) presenting the first assessment of short-term impacts of simultaneous changes in water temperature, flow and dissolved oxygen on behavioural responses of three lowland benthic invertebrate species. The key research outcomes are as follows:

a) **Chapter 2**: The majority of the analysed sites have undergone significant warming in the past 25 years in Germany, with the following significant controls identified at the regional scale:
    i. Air temperature increase is the major driver of increasing river temperature and of river temperature variability at most of the studied sites, with its influence increasing with increasing catchment area and at lower altitudes.
    ii. Flow was identified as the second most important control of river temperature variability, and its contribution in river warming was more important for areas with low water availability (specific runoff).
    iii. Landscape variables such as altitude, catchment area and ecoregion induced spatial variability in the magnitude of river temperature changes via affecting the sensitivity of river temperature to its local climate.
    iv. The length of the study period has a significant impact on the direction and rate of temperature change. Trends identified for short time series of different lengths or different start and end years are difficult to compare.

b) **Chapter 3**: The presence of urban areas and lakes were the most important variables causing spatial river temperature heterogeneity within the ~200 km reach of a lowland river. On the contrary, whereas riparian buffer only had very limited effect on the river temperature.

   i. Urban areas and lakes acted as a heat source, in particular, during the summer months. The impact of urban area on river temperature did not depend on the lateral spatial extent along the river, at least when present within 1 km from the river edge.

   ii. Riparian shading, even when present at up to 20 km longitudinally, reduced maximum river temperatures only by 1°C below lakes, mainly because of the influence of advected heat from the upstream lake which lasts over long distances. This questions the efficacy of riparian shading in moderating river temperatures in such reaches.

   iii. In general, upstream conditions determined the base (or average) river temperature at a site, while climatological variations caused deviations around the base temperature.

c) **Chapter 4**: The three macroinvertebrate species showed different behavioural responses to stressful conditions (such as high temperature, low flow, low dissolved oxygen levels) and not necessarily with drift. Main effects of water temperature and flow were significant for two out of three species for paired stressor combinations whereas the applied low dissolved oxygen levels only produced a significant response when combined with other stressors. Interaction between variables was detected only for temperature and dissolved oxygen for a single species (*Dikerogammarus haemobaphes*), with low dissolved oxygen amplifying the negative impacts of high water temperature.

5.3 Synthesis

5.3.1 Temporal and spatial heterogeneity in river temperature behaviour

Temperature at a particular point in space and time in a channel is a function of heat load and river flow or volume (Poole and Berman, 2001). Variations in heat exchange processes and the volume of water in a channel can determine short-term and long-term trajectories of river water temperature. The results of this study revealed considerable spatial heterogeneity in temporal river temperature behaviour at both regional and reach scales within Germany. At the regional scale, a majority of the analysed sites on northern German rivers showed a long-term increase in river temperature over time, while a minority showed a decrease (Chapter 2). A similar pattern was observed at seasonal and decadal time scales, as river temperature increased for most of the sites across all seasons and decades. The observed temporal changes in river temperature were attributed to temporal changes in air temperature in general, as air temperature also exhibited increasing trends and was the major control of seasonal and annual variability in river temperature. Air temperature change has been observed to the major driver of river temperature change for several other rivers in North America and Europe as well (Webb and Nobilis, 2007; Kaushal *et al.*, 2010; Orr *et al.*, 2014; Rice and Jastram, 2015). The other climatic variable, North Atlantic Oscillation (NAO), which dictates much of the winter variability in air temperature in the Northern Hemisphere (Hurrell, 2003), had a considerable indirect influence on the inter-annual winter variability in river temperature and possibly influenced changes in water temperature during the first decade (1985-1995). River flow was found to have a significant influence on seasonal variability of river temperature over both long and short time periods. Flow is generally seen to have an inverse relationship with water temperature (Chapter 2 and 3; Webb *et al.*, 2003; van Vliet *et al.*, 2011), with greater flows leading to cooler water temperatures. However, the role of increasing flows in moderating the rate of river temperature change over a long time period and at a large spatial scale was indiscernible (Chapter 2), as the greatest impact of flow is seen at shorter time scales (Webb *et al.*, 2003) and declines for very large catchments (Gu *et al.*, 1998). Flow reductions (i.e. reduction in thermal or assimilative capacity of rivers) were suggested to have a clearer influence on long-term river warming at smaller spatial scales (e.g., NE German rivers, Chapter 2; van Vliet *et al.*, 2011). Spatial heterogeneity in the magnitude of long term river temperature change was mostly controlled by spatial differences in altitude, ecoregion and catchment area. Higher river thermal sensitivity (thereby greater river warming) was observed within larger catchment areas and at lower altitudes (lowland rivers), as thermal sensitivity is a function of river size, velocity and water volume (Webb *et al.*, 2008; Kelleher *et al.*, 2012). Higher residence times (quicker rate of reaching equilibrium with air temperatures) and the effect of upstream advected heat (accumulation of the heat in the entire stream network; Chapter 3) contribute to high thermal sensitivity of lowland rivers.

At the reach scale, i.e., within a 200 km reach of a lowland river, the investigated sites showed similar temporal behaviour over a period of nine months (Chapter 3). Among the hydro-climatological variables, air temperature was the major control of river temperature, similar to what observed at the regional scale (Chapter 2). Weaker air-water temperature correlations were observed in the downstream direction, primarily as the heat advected from the upstream reaches becomes more dominant part of the heat content in the channel. Spatial heterogeneity was observed in the magnitude of daily and monthly means of river temperature along the reach, which was mainly attributed to landscape variables. Spatial location of urban areas and lakes defined the spatial heterogeneity within the reach (rather than presence of riparian buffer), as sub-reaches flowing through these structures were warmer in general and also attained the highest maximum temperatures as compared to the sub-reaches without them. Urban areas act as a heat source as the air and ground temperature tend to be higher than in rural areas and also due to warm water additions from industries and runoff from hot pavements (Pickett *et al.*, 2001; Somers *et al.*, 2013). Shallow lakes, such as those found in the study reach, present a greater surface area to volume ratio and a longer residence time (compared to rivers) for receiving atmospheric heat inputs, thereby reaching equilibrium with atmospheric conditions at a faster rate. Additionally, water temperatures at lake outlets are more influenced by water temperature of the much shallower lakeshore. Although the proportion of riparian buffer was negatively correlated with river temperature, the effective buffer width was unclear. Also, riparian buffer did not appear to effectively reduce the maximum and mean temperature below lake affected sub-reaches, mainly as the influence of heat advected from lakes lasts over large distances (at least ~20 km).

5.3.2 River temperature in a multiple stressor context

As especially observed for the lowland rivers in Germany, rising river temperatures are majorly a result of high sensitivity to warmer air temperatures, supplemented by reducing flows, particularly summer flows (Chapter 2; van Vliet *et al.*, 2011). Water temperatures can reach critically high values for freshwater biodiversity during such conditions. In presence of multiple stressors such as reduced flows and dissolved oxygen levels, water temperature has the greatest influence as compared to the other two variables on the behavioural response of freshwater macroinvertebrates (*Hydropsyche pellucidula*, *Calopteryx splendens*, *Dikerogammarus haemobaphes*) on short time scales (Chapter 4). This result particularly highlights the importance of heat-related extreme events, where high temperatures are experienced for short time periods. The behavioural responses of the three macoinvertebrates to stress differed among species, with *H. pellucidula* responding by drifting, *C. splendens* responding by inactivity and *D. haemobaphes* responding by increased locomotion. Among coupled variable effects, the results indicated that concomitant variation of water temperature and flow will have stronger impacts than when temperature and DO or flow and DO vary together. The interactive effects of these variables are, however, highly dependent on the physiological and behavioural traits of a species, and on the stress level involved (Chapter 4).

5.4 Implications for river ecosystem management

Results from the research presented in this thesis add to the growing consensus that river warming is a global phenomenon. Climate change is not suggested to be the sole reason for the observed warming and is rather a result of complex interactions between climate patterns, anthropogenic activities and sensitivity of a river to its environment (Chapter 2; Hannah *et al.*, 2015). Thermal and hydrological regime changes due to changing climate and human activities are one of the major factors threatening the functioning of freshwater ecosystems and the services they provide (Fig. V.1). More specifically, the greatest impacts can be expected during low flows and increased water temperature conditions (Chapter 4; van Vliet *et al.*, 2011), such as those observed for some large lowland rivers in Germany (Chapter 2). Studies have suggested that an increased frequency of low flow and increased water temperature combinations can be expected in the future for Central European rivers (van Vliet *et al.*, 2013). A further concern is the increase in frequency of extreme hydro-climatic events such as heat waves, droughts, floods, which are also expected to occur more frequently in the future (IPCC, 2013). Several German rivers have already seen an increase in the frequency of warm water events since 1985 (Chapter 2). Such events are also likely to have profound and complex consequences for aquatic ecosystems (Lake, 2011). Impacts of co-occurring extreme events may lead to abrupt changes in species compositions and distributions and may affect future responses of the ecosystem to similar events (Leigh *et al.* 2014). The results presented in this thesis suggest that when a heat wave (high water temperature) is accompanied by drought-like conditions (low flow) for short periods of time, the effect of the heat wave may override the low flow effects or low flow effects might dominate or act along with heat wave effects, depending on the species (Chapter 4).

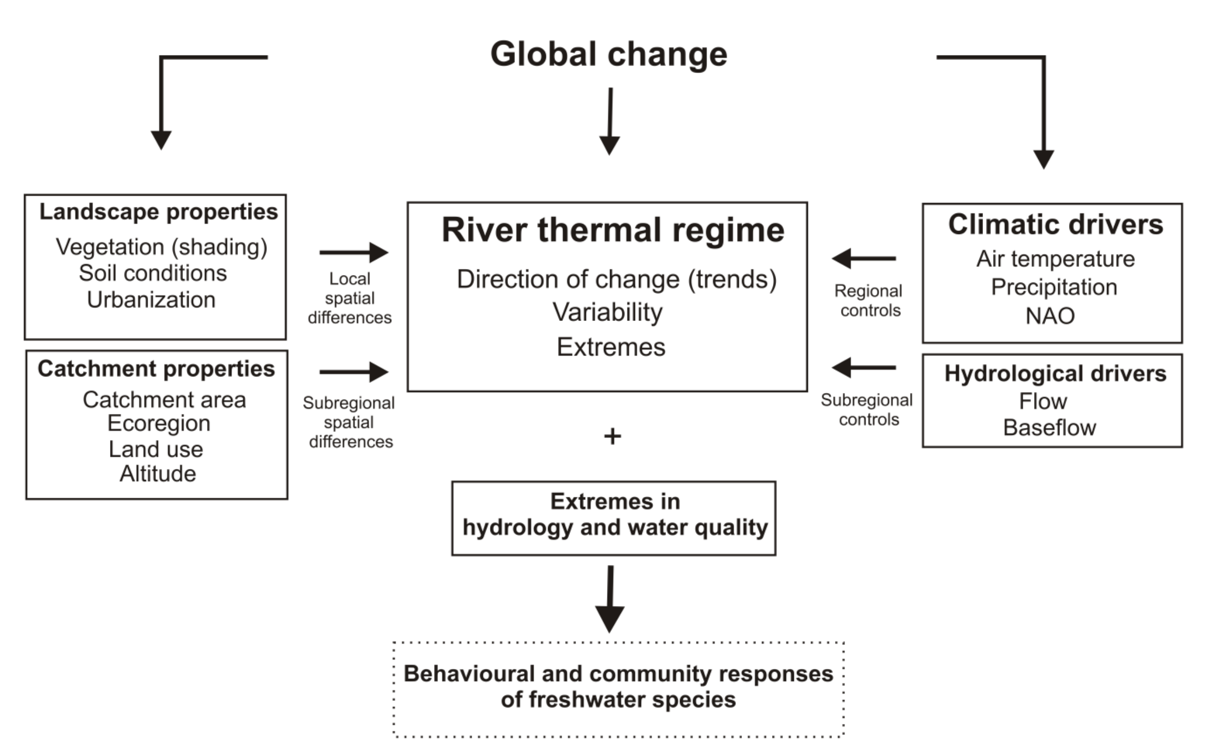

Figure V.1 Synthesis of the findings from the thesis showing the major variables affecting river thermal regime and, thereby, the freshwater ecosystem. Climatic drivers such as air temperature exert major controls on river temperature and act at regional scales while hydrological controls, such as flow, act sub-regionally, having a substantial influence on river temperature variability. Landscape and catchment properties induce local and sub-regional spatial differences in climate, hydrology and river morphology and thereby, river thermal regimes. Global changes caused by human activities can affect river thermal regimes directly as well indirectly via affecting any one or more of the mentioned controls. Extremes in river temperatures and other important water quality parameters, such as flow and dissolved oxygen, due to such environmental changes can induce several behavioural responses in freshwater species, ultimately affecting the entire ecosystem as a whole.

A major proportion of (60% of 1648 species) European freshwater species is expected to lose at least 50% of their suitable habitat by 2050 due to climate change impacts, including river warming (Markovic *et al.*, 2014). The results from this research suggest that river temperature behaviour of lowland rivers is the most susceptible to changing climate (Chapter 2). Lowland rivers, such as River Spree, are further subjected to additional pressures such as local impacts of urbanization, discharge of warm water from shallow lakes and the cumulative effect of advected heat (Chapter 3). Therefore, urgent measures are needed to prevent or reduce the effect of environmental change on river temperatures. Several measures have been suggested in the literature to reduce river water temperatures. They include riparian buffer plantation

(Hrachowitz *et al.*, 2010; Broadmeadow *et al.*, 2011; Imholt *et al.*, 2013; Garner, 2014), restoration of floodplain connectivity and natural channel geomorphology (Poole and Berman, 2001), cold water releases from reservoirs (Isaak *et al.*, 2012), and increase in discharge/decrease in abstraction (Gu *et al.*, 1998; Poole and Berman, 2001). Riparian buffer plantation is widely recognized as a possible climate adaptation option by the forestry sector in North America and, more recently, in the UK as well (Johnson and Wilby, 2015). For headwater rivers, riparian buffers have been suggested to be most effective in moderating maximum water temperatures (Hrachowitz *et al.*, 2010; Garner, 2014). For mid-sized to large lowland rivers, the efficacy of riparian buffer is reduced or negligible as the canopy cover is unable to effectively shade these rivers due to increased river width. Plantation of riparian buffers along headwater rivers has also been suggested to contribute to lower water temperature in the lowland rivers and also throughout river basins (Hrachowitz *et al.*, 2010; Garner, 2014). However, this would probably be less effective for lowland rivers where buffer areas are dominated by urban cover and those flowing through shallow lakes, as these structures have been observed to cause warmer river temperatures (Chapter 3; Mellina *et al.*, 2002; Somers *et al.*, 2013; Booth *et al.*, 2014). Also, riparian buffers were observed not to be very effective in reducing water temperatures below lakes as the heat advected from the lakes plays a more dominating influence (Chapter 3).

Therefore, for lowland rivers in general, river temperature could be managed through flow manipulation (prevention of low flows), sustainable waste water inputs, through the restoration and plantation of riparian buffers (for small lowland rivers) and through the protection and conservation of high altitude rivers (e.g. via flow protection and riparian buffer plantation), as river temperature response in lowland catchments is a combination of local as well as upstream conditions. For lowland reaches influenced by shallow lentic structures and urban areas, additional or alternative measures such as improving the groundwater recharge, managing the temperature of urban discharges or creating shaded artificial ponds may be more effective and are thus suggested.

References

ADV, 2012. *Arbeitsgemeinschaft der Vermessungs-verwaltungen der Länder der Bundesrepublik Deutschland: Erläuterungen zum ATKIS-Objektartenkatalog der Arbeitsgemeinschaft der Vermessungsverwaltungen der Länder der Bundesrepublik Deutschland*. Available at: http://www.adv-online.de/Geotopography/ATKIS/

Alvarez D, Nicieza AG.2005. Compensatory response 'defends' energy levels but not growth trajectories in brown trout, Salmo trutta L. *Proceedings of the Royal Society B: Biological Sciences* **272**: 601–607

Apodaca CK, Chapman LJ. 2004. Larval damselflies in extreme environments: Behavioral and physiological response to hypoxic stress. *Journal of Insect Physiology* **50** (9): 767–775

Arismendi I, Johnson SL, Dunham JB, Haggerty R, Hockman-Wert D. 2012. The paradox of cooling streams in a warming world: Regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* **39,** L10401.

Arismendi I, Safeeq M, Dunham JB, Johnson SL. 2014. Can air temperature be used to project in fl uences of climate change on stream temperature ? *Environmental Research Letters* **9**(8): 084015

Arnell NW, Gosling, SN. 2013. The impacts of climate change on river flow regimes at the global scale. *Journal of Hydrology* **486**:351-364.

Arscott DB, Tockner K, Ward J V. 2001. Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). *Canadian Journal of Fisheries and Aquatic Sciences* **58** (12): 2359–2373.

Ashizawa D, Cole JJ. 1994. Long-term temperature trends for the Hudson River: a study of the historical data. *Estuaries* **17**(1): 166–71.

Bärlocher F, Seena S, Wilson KP, Williams DD. 2008. Raised water temperature lowers diversity of hyporheic aquatic hyphomycetes. *Freshwater Biology* **53**:368–379.

Benson NG. 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. (Ed J.B. Trefethen) In: *Transactions of the Eighteenth North American Wildlife Conference*, pp. 269–281, Washington, DC, March 9, 10, and 11, 1953. Wildlife Management Institute, Wire Building, Washington 5, DC.

Benyahya L, Caissie D, St-hilaire A, Ouarda TBMJ, Bobée B. 2007. A Review of Statistical Water Temperature Models. *Canadian Water Resources Journal* **32**(3): 179–192

Boets P, Lock K, Messiaen M, Goethals PL. 2010. Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. *Ecological Informatics* **5**(2), 133-139.

Booth DB, Kraseski KA, Rhett JC. 2014. Local-scale and watershed-scale determinants of summertime urban stream temperatures. *Hydrological Processes* **28**(4): 2427–2438.

Bormann H. 2010. Runoff regime changes in German rivers due to climate change. *Erdkunde* **64**(3):257-279.

Boyd WA, Brewer SK, Williams PL. 2002. *Chapter 8: Altered Behaviour of Invertebrates Living in Polluted Environments. In: Behavioural ecotoxicology* by Dell'Omo, G. John Wiley & Sons.

Brezonik PL. 1972. *Chemical kinetics and dynamics in natural water systems. In :Ciaccio, L.L. (Ed.), Water and Wafer Pollution Handbook*. Vol. 3. Marcel Dekker, New York. pp. 831-913.

Brittain JE, Eikeland TJ. 1988. Invertebrate drift - A review. *Hydrobiologia* **166**:77–93.

Broadmeadow SB, Jones JG, Langford TEL, Shaw PJ, Nisbet TR. 2011. The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. River *Research and Applications* **27**: 226–237.

Brown GW, Krygier JT. 1970. Effects of clear-cutting on stream temperature. *Water Resources Research* **6:**1133–1139.

Brown GW. 1969. Predicting temperatures of small streams. *Water Resources Research* **5**:68–75.

Brown LE, Hannah DM, MilnerAM. 2007. Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology* **13**:958–966.

Brunke M, Hoffmann A, Pusch M. 2001. Use of mesohabitat-specific relationships between flow velocity and river discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research and Management* **17**: 667–676

Bruno MC, Siviglia a., Carolli M, Maiolini B. 2013. Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology* **6**(4): 511–522 .

Burgmer T, Hillebrand H, Pfenninger M. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia* **151**(1): 93–103.

Caissie D. 2006. The thermal regime of rivers : a review. *Freshwater Biology* **51**: 1389–1406.

Caldwell P, Segura C, Laird SG, Sun G, McNulty SG, Sandercock M, Boggs J, Vose JM. 2015. Short-term stream water temperature observations permit rapid assessment of potential climate change impacts. *Hydrological Processes* **29**(9):2196–2211.

Chadwick MA, Feminella JW. 2001. Influence of salinity and temperature on the growth and production of a freshwater mayfly in the Lower Mobile River, Alabama. *Limnology and Oceanography* **46**:532–542

Chang H, Lawler K. 2011. Impacts of Climate Variability and Change on Water Temperature in an Urbanizing Oregon Basin, USA. *Water Quality: Current Trends and Expected Climate Change Impacts* **348**: 123–128

Chessman BC. 2009. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Global Change Biology* **15**(11): 2791–2802.

Chessman BC. 2015. Relationships between lotic macroinvertebrate traits and responses to extreme drought. *Freshwater Biology* **60**: 50–63.

Connolly NM, Crossland MR, Pearson RG. 2004. Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. *Journal of North American Benthological Society* **23**(2): 251–270.

Dang CK, Harrison S, Sturt MM, Giller PS, Jansen MAK. 2009. Is the elemental com- position of stream invertebrates a determinant of tolerance to organic pollution? *Journal of the North American Benthological Society* **28**:778–784

Daufresne M, Roger MC, Capra H, Lamouroux N. 2004. Long-term changes within the invertebrate and fish communities of the Upper Rhone River: Effects of climatic factors. *Global Change Biology* **10**(1): 124–140.

Dewson ZS, James ABW, Death RG. 2007a. A review of the consequences of decreased flow for instream habitat and macroinvertebrates A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* **26**(3): 401–415

Dewson ZS, James ABW, Death RG. 2007b. Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology* **52**(2): 357–369.

Dohet A, Hlúbiková D, Wetzel CE, L'Hoste L, Iffly JF, Hoffmann L, Ector L. 2015. Influence of thermal regime and land use on benthic invertebrate communities inhabiting headwater streams exposed to contrasted shading. *Science of the Total Environment* **505**:1112-1126.

Dorier A, Vaillant F. 1953/1954. Observations et expériences relatives à la résistance au courant de divers in- vertébrés aquatiques. *Extrait de la Laboratoire de Hydrobiologie et Pisciculture Grenoble* **45/46**: 9-31.

Ducharne A, 2008. Importance of Stream Temperature to Climate Change Impact on Water Quality. *Hydrology and Earth System Sciences* **12**(3):797-810.

Durance I, Ormerod SJ. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* **13**(5): 942–957.

Durance I, Ormerod SJ. 2009. Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshwater Biology* **54**(2): 388–405.

DWD – Deutscher Wetterdienst.2015. *Zahlen und fakten zum klimawandel in Deutschland. Klima-pressekonferenz des Deutschen Wetterdienstes am 10. März 2015 in Berlin* . http://www.dwd.de/bvbw/generator/DWDWWW/Content/Presse/Pressekonferenzen/2015/PK__10__03-2015/ZundF__zur__PK,templateId=raw,property=publicationFile.pdf/ZundF_zur_PK.pdf

Edington JM. 1965. Some observations on stream temperature. *Oikos* **1:**265-273.

EEA-European Environment Agency, 2008b. *Impacts of Europe's Changing Climate – Indicator-based Assessment. EEA, Copenhagen*. EEA Report No 4/2008, ISSN 1725-9177. https://ec.europa.eu/jrc/sites/default/files/jrc_reference_report_2008_09_climate_change.pdf

Elliott, JM, Hurley, MA, Maberly, SC. 2000. The emergence period of sea trout fry in a Lake District stream correlates with the North Atlantic Oscillation. *Journal of Fish Biology* **56**:208–210.

Erickson TR, Stefan HG. 2000. Linear air/water temperature correlations for streams during open water periods. *Journal of Hydrologic Engineering* **5**(3): 317–321.

Floury M, Usseglio-Polatera P, Ferreol M, Delattre C, Souchon Y. 2013. Global climate change in large European rivers: long-term effects on macroinvertebrate communities and potential local confounding factors. *Global change biology* **19**(4): 1085–99.

Floury M, Delattre C, Ormerod SJ, Souchon Y. 2012. Global versus local change effects on a large European river. *Science of the total environment* **441**:220-229.

Friberg N, Christensen JB, Olafsson JS, Gislason GM, Larsen SE, Lauridsen TL. 2009. Relationship between structure and function in streams contrasting in temperature: possible impacts of climate change on running water ecosystems. *Freshwater Biology* **54:**2051–2206.

Gabel F, Pusch MT, Breyer P, Burmester V, Walz N, Garcia X-F. 2011. Differential effect of wave stress on the physiology and behaviour of native versus non-native benthic invertebrates. *Biological Invasions* **13** (8): 1843–1853

Garner G.2014. *River and stream temperature in a changing climate*. Ph. D thesis, University of Birmingham, United Kingdom.

Garner G, Hannah DM, Sadler JP, Orr HG. 2013. River temperature regimes of England and Wales: spatial patterns, inter-annual variability and climatic sensitivity. *Hydrological Processes* **28**(22): 5583-5598.

Gerhardt, A. (1996). Behavioural early warning responses to polluted water. *Environmental Science and Pollution Research* **3**(2): 63-70.

Gibbins CN, Vericat D, Batalla RJ. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. *Journal of the North American Benthological Society* **29**(3):945-958.

Gibson RJ. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. *Journal of the Fisheries Research Board of Canada* **23**:1977–1980.

Golyandina N, Nekrutkin V, Zhigljavsky A. 2010. *Analysis of time series structure: SSA and related techniques*. CRC press LLC, Florida, USA.

Golyandina N, Zhigljavsky A. 2012, 2014. Basic singular spectrum analysis and forecasting with R. *Computational Statistics and Data Analysis* **71**: 934:954. http://arxiv.org/abs/1206.6910

Gordon, DM. 2011. The fusion of behavioral ecology and ecology. *Behavioral Ecology* **22**(2):225-230.

Graeber D, Pusch MT, Lorenz S, Brauns M. 2013. Cascading effects of flow reduction on the benthic invertebrate community in a lowland river. *Hydrobiologia* **717** (1): 147–159.

Gray JRA, Edington JM. 1969. Effect of woodland clearance on stream temperature. *Journal of the Fisheries Research Board of Canada* **26**:399–403

Gu R, Montgomery S, Austin TAL. 1998. Quantifying the effects of stream discharge on summer river temperature. *Hydrological Sciences* **43**(6): 885–904

Haidekker A, Hering D. 2008. Relationship between benthic insects (Ephemeroptera , Plecoptera , Coleoptera , Trichoptera) and temperature in small and medium-sized streams in Germany : A multivariate study. *Aquatic Ecology* **42**: 463–481.

Hannah DM, Garner G. 2015. River water temperature in the United Kingdom: changes over the 20th century and possible changes over the 21st century. *Progress in Physical Geography* **39** (1): 68–92.

Hannah DM, Malcolm I a., Soulsby C, Youngson AF. 2004. Heat exchanges and temperatures within a salmon spawning stream in the Cairngorms, Scotland: seasonal and sub-seasonal dynamics. *River Research and Applications* **20**(6): 635–652

Hannah DM, Malcolm IA, Soulsby C, Youngson AF. 2008a. A comparison of forest and moorland stream microclimate, heat exchanges and thermal dynamics. *Hydrological processes* **22**: 919–940.

Hannah DM, Webb BW, Nobilis F. 2008b. River and stream temperature : dynamics, processes, models and implications – preface. *Hydrological Processes* **22**: 899–901.

Hardewig I, Pörtner HO, Van Dijk P. 2004. How does the cold stenothermal gadoid *Lota lota* survive high water temperatures during summer?. *Journal of Comparative Physiology B* **174**(2), 149-156.

Hari RE, Livingstone DM, Siber R, Burkhardt-Holm P, Guttinger H (2006) Consequences of climatic change for water temperature and brown trout populations in alpine rivers and streams. *Global Change Biology* **12**:10–26

Hebert C, Caissie D, Satish MG, El-Jabi N. 2011. Study of stream temperature dynamics and corresponding heat fluxes within Miramichi River catchments (New Brunswick, Canada). *Hydrological Processes* **25** (15): 2439–2455

Hester ET, Bauman KS. 2013. Stream and Retention Pond Thermal Response to Heated Summer Runoff From Urban Impervious Surfaces. *Journal of the American Water Resources Association* **49** (2): 328–342

Hill RA, Hawkins CP, Jin J. 2014. Predicting thermal vulnerability of stream and river ecosystems to climate change. *Climatic Change* **125**(3-4):399–412.

Hogg ID, Williams DD. 1996. Response of Stream Invertebrates to a Global-Warming Thermal Regime : An Ecosystem-Level Manipulation. *Ecology* **77**(2): 395–407.

Hölzel H, Gädeke A, Koch H, Grünewald U. 2012. Assessment of climate change impacts on hydrological processes and patterns in the Spree River catchment. *Geophysical Research Abstracts* **14**:EGU2012-2321-1.

Hrachowitz M, Soulsby C, Imholt C, Malcolm I a., Tetzlaff D. 2010. Thermal regimes in a large upland salmon river: a simple model to identify the influence of landscape controls and climate change on maximum temperatures. *Hydrological Processes* **24**(23): 3374–3391.

Huang S, Krysanova V, Hattermann FF. 2012. *Impacts of Climate Change on Water availability and Crop Yield in Germany*. International congress on environmental modelling and software managing resources of a limited planet, Sixth biennial meeting, Leipzig, Germany.

Hurrell JW (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**:676–679.

Imboden, D. M., & Wüest, A. (1995*). Mixing mechanisms in lakes*. In: *Physics and chemistry of lakes* (pp. 83-138). Springer Berlin Heidelberg.

Imholt C, Soulsby C, Malcolm IA, Hrachowitz M, Gibbins CN, Langan S, Tetzlaff D. 2013. Influence of scale on thermal characteristics in a large montane river basin. *River Research and Applications* **29**(1): 403–419.

IPCC, 2013: Climate Change 2013: Technical Summary. In: Climate Change 2013: *The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Isaak DJ, Hubert WA .2001. A hypothesis about factors that affect maximum summer stream temperatures across montane landscapes. *Journal of the American Water Resources Association* **37**: 351–366.

Isaak DJ, Rieman BE. 2013. Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology* **19**: 742–751.

Isaak DJ, Wollrab S, Horan D, Chandler G. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change* **113**: 499–524.

Jacobsen D, Schultz R, Encalada A. 1997. Structure and diversity of stream invertebrate assemblages : the influence of temperature with altitude and latitude. *Freshwater Biology* **38**: 247–261.

Johnson B, Johnson N .2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology* **75**(10): 2381–2447.

Johnson MF, Wilby RL, Toone J a. 2014. Inferring air-water temperature relationships from river and catchment properties. *Hydrological Processes* **28**: 2912–2928.

Johnson MF, Wilby RL. 2015. Seeing the landscape for the trees:Metrics to guide riparian shademanagement in river catchments. *Water Resources Research* **51**: 446

Johnson, JL, Stefan HG. 2006. Indicators of climate warming in Minnesota: Lake ice covers and snowmelt runoff. *Climatic Change* **75**(4): 421-453.

Justus BG, Mize SV, Wallace J, Kroes D. 2014. Invertebrate and fish assemblage relations to dissolved oxygen minima in lowland streams of southwestern Louisiana. *River Research and Applications* **30**(1):11-28.

Kaltofen M, Koch H, Schramm M. 2008. *Water management strategies in the Spree region upstream of Berlin*. In: Wechsung, Kaden, Behrendt & Klöcking (eds.): *Integrated Analysis of the Impacts of Global Change on Environment and Society in the Elbe River Basin*. Weißensee-Verlag Berlin, S. 236-253.

Karl TR, Arguez A, Huang B, Lawrimore JH, McMahon, JR, Menne MJ, Peterson TC, Vose RS, Zhang HM. 2015. Possible artifacts of data biases in the recent global surface warming hiatus. *Science* **348**(6242):1469-1472.

Kaushal SS, Likens GE, Jaworski NA, Pace ML, Ashley M, Seekell D, Belt KT, Secor DH, Wingate RL, Sides AM. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* **8**(9): 461–466

Kelleher C, Wagener T, Gooseff M, McGlynn B, McGuire K, Marshall L. 2012. Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes* **26**(5): 771–785.

Kinouchi T, Yagi H, Miyamoto M. 2007. Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology* **335**(1-2): 78–88.

Kishi D, Murakami M, Nakano S, Maekawa K. 2005. Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology* **50**(8): 1315–1322.

Kititsyna LA. 1980. Ecological and physiological pecularities of Dikerogammarus haemobaphes (Eichw.) in the region of the Tripolye State Supercentral Electric Station heated water discharge. *Gidrobiologicheskij Zhurnal* **16**: 77-85.

Koch H, Grünewald U. 2010. Regression models for daily stream temperature simulation: case studies for the river Elbe, Germany. *Hydrological Processes* **24**(26): 3826–3836.

Kozerski HP, Köhler J, Schellenberger G. 1991. *Transport of particulate nutrients and pollutants in the lowland River Spree*. In: *Sediment and steam water quality in a changing environment: trends and explanation*. Proceedings of a symposium held during the XXth General Assembly of the International Union of Geodesy and Geophysics, Vienna, Austria (pp. 11-24).

Lake PS. 2011. *Drought and Aquatic Ecosystems: Effects and Responses*. Wiley-Blackwell, Chichester, U.K.

Lamberti GA, Resh VH. 1983. Geothermal effects on stream benthos: separate influences of thermal and chemical components on periphyton and macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **40**(11):1995-2009.

Leach JA , Moore RD. 2011. Stream temperature dynamics in two hydrogeomorphically distinct reaches. *Hydrological Processes* **25**: 679–690.

LeBlanc RT, Brown RD, FitzGibbon JE. 1997. Modeling the Effects of Land Use Change on the Water Temperature in Unregulated Urban Streams. *Journal of Environmental Management* **49** (4): 445–469.

Lecerf A, Risnoveanu G, Popescu C, Gessner MO, Chauvet E. 2007. Decomposition of diverse litter mixtures in streams. *Ecology* **88**:219–227.

Ledger ME, Brown LE, Edwards FK, Milner AM, Woodward G. 2013. Drought alters the structure and functioning of complex food webs. *Nature Climate Change* **3**:223–227.

Leigh C, Bush A, Harrison ET, Ho SS, Luke L, Rolls RJ, Ledger ME. 2014. Ecological effects of extreme climatic events on riverine ecosystems : insights from Australia. *Freshwater Biology* **60**:2620-2638.

Liebmann, B, Dole RM, Jones C, Blade I, Allured D. 2010. Influence of choice of time period on global surface temperature trend estimates. *Bulletin of the American Meteorological Society* **91**: 1485–1491.

Maazouzi C, Piscart C, Legier F, Hervant F. 2011. Ecophysiological responses to temperature of the 'killer shrimp' Dikerogammarus villosus: is the invader really stronger than the native Gammarus pulex? *Comparative biochemistry and physiology Part A* **159**(3): 268–274.

Macan TT. 1958. The temperature of a small stony stream. *Hydrobiologia* **12**:89–106.

Malcolm IA, Soulsby C, Hannah DM, Bacon PJ, Youngson AF, Tetzlaff D. 2008. The influence of riparian woodland on stream temperatures : implications for the performance of juvenile salmonids. *Hydrolgical processes* **22**: 968–979.

Markovic D, Carrizo S, Freyhof J, Cid N, Lengyel S, Scholz M, Kasperdius H, Darwall W. 2014. Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions* **20** (9): 1097–1107.

Markovic D, Scharfenberger U, Schmutz S, Pletterbauer F, Wolter C. 2013. Variability and alterations of water temperatures across the Elbe and Danube River Basins. *Climatic Change* **119**(2): 375–389.

Martin JL, McCutcheon, S. C. (1998). Chapter 8:Stratification and heat transfer in lakes and reservoirs: In *Hydrodynamics and transport for water quality modeling*. CRC Press, Chicago.

Mayer TD. 2012. Controls of summer stream temperature in the Pacific Northwest. *Journal of Hydrology* **475**: 323–335.

Mellina E, Moore RD, Hinch SG, Macdonald JS, Pearson G. 2002. Stream temperature responses to clearcut logging in British Columbia : the moderating influences of groundwater and headwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1886–1900.

Miller, P. L. (1993). Responses of rectal pumping to oxygen lack by larval Calopteryx splendens (Zygoptera: Odonata). *Physiological entomology* **18**(4):379-388.

Moatar F, Gailhard J. 2006. Water temperature behaviour in the River Loire since 1976 and 1881. *Comptes Rendus Geoscience* **338**: 319-328.

Mohseni O, Stefan HG. 1999. Stream temperature/air temperature relationship: a physical interpretation. *Journal of Hydrology* **218** (3-4): 128–141.

Montgomery DR.. 1999. Process Domains and the River Continuum. *Journal of the American Water Resources Association* **35**:397-410.

Moore RD, Spittlehouse DL, Story A. 2005. Riparian microclimate and stream temperature response to forest harvesting: A review. *Journal of American Water Resources Association* **41**(4): 813–834.

Morrill JC, Bales RC, Conklin MH. 2005. Estimating Stream Temperature from Air Temperature: Implications for Future Water Quality. *Journal of Environmental Engineering* **131** (1): 139–146.

Morse, W. L. 1970. Stream temperature prediction model. *Water Resources Research* **6**(1):290-302.

Neal C, Bowes M, Jarvie HP, Scholefield P, Leeks G, Neal M, Rowland P, Wickham H, Harman H, Armstring L, Sleep D. (2012) Lowland river water quality: a new UK data resource for process and environmental management analysis. *Hydrological Processes* **26**:949–960.

Nelson KC, Palmer MA. 2007. Stream temperature surges under urbanization. *Journal of American Water Resources Association* **43**(2): 440–452.

Norris RH, Thoms MC. 1999. What is river health?. *Freshwater Biology* **41**(2): 197-209.

Ormerod SJ, Dobson M, Hildrew AG, Townsend CR. 2010. Multiple stressors in freshwater ecosystems. *Freshwater Biology* **55**(SUPPL. 1): 1–4.

Orr HG, Simpson GL, des Clers S, Watts G, Hughes M, Hannaford J, Dunbar MJ, Laizé CLR, Wilby RL, Battarbee RW, et al. 2014. Detecting changing river temperatures in England and Wales. *Hydrological Processes* **29**:752-766.

Pedersen NL, Sand-Jensen K. 2007. Temperature in lowland Danish streams : contemporary patterns , empirical models and future scenarios. *Hydrological Processes* **21**: 348–358.

Pekarova P, Halmova D, Miklanek P, Onderka M, Pekar J, Skoda P. 2008. Is the Water Temperature of the Danube River at Bratislava, Slovakia, Rising?. *Journal of Hydrometeorology* **9**(5):1115-1122.

Pekárová P, Miklánek P, Halmová D, Onderka M, Pekár J, Kučárová K, Liová S, Škoda P. 2011. Long-term trend and multi-annual variability of water temperature in the pristine Bela River basin (Slovakia). *Journal of Hydrology* **400**(3): 333-340.

Petersen JH, Kitchell JF. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1831–1841.

Philipson GN, Moorhouse BHS. 1974. Observations on ventilatory and net-spinning activities of larvae of the genus Hydropsyche Pictet (Trichoptera , Hydropsychidae) under experimental conditions. *Freshwater Biology* **4**: 525–533

Piccolroaz S, Toffolon M, Majone B. 2013. A simple lumped model to convert air temperature into surface water temperature in lakes. *Hydrology and Earth System Sciences* **17**:3323-3338.

Piccolroaz S, Toffolon M, Majone B. 2015. The role of stratification on lakes' thermal response: The case of Lake Superior. *Water Resources Research* doi:10.1002/2014WR016555.

Piccolroaz S, Calamita E, Majone B, Siviglia A, Gallice A, Toffolon M. Prediction of river water temperature: a comparison between a new family of hybrid models and statistical approaches, submitted to Hydrological Processes.

Pickett ST, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R. 2008. *Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas*. In*: Urban Ecology* (pp. 99-122). Springer US.

Piggott JJ, Salis RK, Lear G, Townsend CR, Matthaei CD. 2015. Climate warming and agricultural stressors interact to determine stream macroinvertebrate community dynamics. *Global Change Biology* **21**: 1887–1906.

Pilgrim JM, Fang X, Stefan HG. 1998. Stream temperature correlations with air temperatures in Minnesota: implications for climate warming. *Journal of the American Water Resources Association* **34**(5): 1109–1121.

Pluhowski EJ. 1970. Urbanization and its effect on the temperature of streams on Long Island, New York. *US Geological Survey Professional Paper* 627-D.

Poff NL, Bledsoe BP, Cuhaciyan CO. 2006. Hydrologic variation with land use across the contiguous United States: geomorphic and ecological consequences for stream ecosystems. *Geomorphology* **79**(3–4): 264–285.

Poole GC, Berman CH. 2001. An Ecological Perspective on In-Stream Temperature: Natural Heat Dynamics and Mechanisms of Human-CausedThermal Degradation. *Environmental Management* **27**(6): 787–802.

Pottgiesser T, Sommerhäuser M. 2004. *Profiles of German Stream Types. Länder-Arbeitsgemeinschaft Wasser (LAWA)*. Umweltbundesamt, Dessau, Germany. Available at: http://www.wasserblick.net/servlet/is/18727/?lang=en

Pusch MT, Hoffmann A. 2000. Conservation concept for a river ecosystem (River Spree, Germany) impacted by flow abstraction in a large post-mining area. *Landscape and Urban Planning* **51**(2):165-176.

Reiter M, Bilby RE, Beech S, Heffner J. 2015. Stream Temperature Patterns over 35 Years in a Managed Forest of Western Washington. *Journal of the American Water Resources Association* **51**(5): 1418-1435.

Rice KC, Jastram JD. 2015. Rising air and stream-water temperatures in Chesapeake Bay region, USA. *Climatic Change* **128**: 127–138.

Sand-Jensen K, Pedersen NL .2005. Differences in temperature, organic carbon and oxygen consumption among lowland streams. *Freshwater Biology* **50**:1927–1937.

Schindler DE, Rogers DE, Scheuerell MD. 2005. Effects of Changing Climate on Zooplankton and Juvenile Sockeye Salmon Growth in Southwestern Alaska. *Ecology* **86**(1):198-209.

Schnauder I, Rudnick S, Garcia X, Aberle J. 2010. *Incipient motion and drift of benthic invertebrates in boundary shear layers*. In: *River Flow*, pp 7-10.

Sherberger FF, Benfield EF, Dickson KL, Cairns Jr J. 1977. Effects of thermal shocks on drifting aquatic insects: a laboratory simulation. *Journal of the Fisheries Board of Canada* **34**(4):529-536.

Smith K. 1972. River water temperatures: an environmental review. *Scottish Geographical Magazine* **88**: 211–220

Somers KA, Bernhardt ES, Grace JB, Hassett BA, Sudduth EB, Wang S, Urban DL. 2013. Streams in the urban heat island: spatial and temporal variability in temperature. *Freshwater Science* **32**(1): 309–326.

Sponseller RA, Benfield EF, Valett HM. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* **46**: 1409–1424.

Stahl K, Hisdal H, Hannaford J, Tallaksen LM, Van Lanen HAJ, Sauquet E, Demuth S, Fendekova M, Jódar J. 2010. Streamflow trends in Europe: evidence from a dataset of near-natural catchments. *Hydrology and Earth System Sciences Discussions* **7**(4): 5769-5804.

Stevens HH, Ficke JE, Smoot GE. 1975. *Water temperature, influential factors, field measurement and data presentation*. In: *Techniques of water-resources investigations of the US Geological Survey*. Book 1, collection of water data by direct measurement, chapter D1, 65 pp

Strayer DL, Dudgeon D. 2010. Freshwater biodiversity conservation : recent progress and future challenges. *Journal of North American Benthological Society* **29** (1): 344–358.

Sun N, Yearsley J, Voisin N, Lettenmaier DP. 2014. A spatially distributed model for the assessment of land use impacts on stream temperature in small urban watersheds. *Hydrological Processes* **29**(10):2331-2345.

Swansburg E, El-Jabi N, Caissie D, Chaput G. 2004. Hydrometeorological trends in the Miramichi river, Canada: implications for Atlantic salmon growth. *North American Journal of Fisheries Management* **24**(2): 561-576.

Tockner K, Uehlinger U, Robinson CT. 2009. *Rivers of Europe*. Academic Press. ISBN-13:978-0-12-369449-2

Tockner K, Pusch MT, Borchardt D, Lorang MS. 2010. Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology* **55**:135-151.

Toffolon M, Piccolroaz S. 2015. A hybrid model for river water temperature as a function of air temperature and discharge. *Environmental Research Letters* **10**(11): 114011.

Toffolon M, Piccolroaz S, Majone B, Soja AM, Peeters F, Schmid M, Wüest A. 2014. Prediction of surface temperature in lakes with different morphology using air temperature. *Limnology and Oceanography* **59**(6):2182-2202.

Townsend CR, Hildrew AG. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *The Journal of Animal Ecology* **45**(3): 759-772

Umweltbundesamt (UBA). 2010. *Impacts of climate change on water resources – adaption strategies for Europe*. Environmental Research of the Federal Ministry of the Environment, Nature Conservation and Nuclear Safety. Research Report 205 21 200, UBA-FB 001175. http://www.umweltbundesamt.de/sites/default/files/medien/publikation/long/3630.pdf

Umweltbundesamt (UBA). 2013. *Ökologischer Zustand der Fließgewässer*. Date of access: 1 March 2015. http://www.umweltbundesamt.de/daten/gewaesserbelastung/fliessgewaesser/oekologischer-zustand-der-fliessgewaesser

van Vliet MTH, Franssen WHP, Yearsley JR, Ludwig F, Haddeland I, Lettenmaier DP, Kabat P. 2013. Global river discharge and water temperature under climate change. *Global Environmental Change* **23**(2): 450–464.

van Vliet MTH, Ludwig F, Zwolsman JJG, Weedon GP, Kabat P. 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. *Water Resources Research* **47**: W02544.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130–137.

Vaughan IP, Ormerod SJ. 2014. Linking interdecadal changes in British river ecosystems to water quality and climate dynamics. *Global Change Biology* **20** (9): 2725–2740.

Verberk WCEP, Bilton DT. 2013. Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters* **9**(5): 20130473

Verberk WCEP, Calosi P. 2012. Oxygen limits heat tolerance and drives heat hardening in the aquatic nymphs of the gill breathing damselfly Calopteryx virgo (Linnaeus, 1758). *Journal of Thermal Biology* **37** (3): 224–229.

Vornanen M, Haverinen J, Egginton S. 2014. Acute heat tolerance of cardiac excitation in the brown trout (Salmo trutta fario). *The Journal of experimental biology* **217**(2):299-309.

Ward J. 1963. Annual variation of stream water tem- perature. *ASCE Journal of the Sanitary Engineering Division* **89**:3710–3732.

Ward JV. 1985. Thermal characteristics of running waters. *Hydrobiologia* **125**:31–46.

Watanabe NC, Mori I, Yoshitaka I (1999) Effect of water temperature on the mass emergence of the mayfly, Ephoron shigae, in a Japanese river (Ephemeroptera: Polymitaryidae). *Freshwater Biology* **41**:537–541.

Webb BW, Zhang Y (1997) Spatial and seasonal variability in the components of the river heat budget. Hydrological Processes 11: 79–101.

Webb BW, Clack PD, Walling DE. 2003. Water-air temperature relationships in a Devon river system and the role of flow. *Hydrological Processes* **17**(15): 3069–3084.

Webb BW, Hannah DM, Moore RD, Brown LE, Nobilis F. 2008. Recent advances in stream and river temperature research. *Hydrological processes* **22**: 902–918.

Webb BW, Nobilis F. 1994. Water temperature behaviour in the River Danube during the twentieth century. *Hydrobiologia* **291**(2): 105–113.

Webb BW, Nobilis F. 1995. Long term water temperature trends in Austrian rivers. *Hydrological Sciences Journal* **40**: 83–96.

Webb BW, Nobilis F. 2007. Long-term changes in river temperature and the influence of climatic and hydrological factors. *Hydrological Sciences Journal* **52**(1): 74–85.

Webb BW, Walling DE. 1992. Long term water temperature behaviour and trends in a Devon, UK, river system. *Hydrological Sciences* **37:** 567-580.

Webb BW. 1996. Trends in stream and river temperature. *Hydrological Processes* **10**(1): 205–226

Wehrly KE, Wang L and MitroM. 2007. Field-based esti- mates of thermal tolerance limits for trout: Incorporat- ing exposure time and temperature fluctuation. *Transactions of the American Fisheries Society* **136**: 365–374.

Wenger SJ, Isaak DJ, Dunham JB, Fausch KD, Luce CH, Neville HM, Rieman BE, Young MK, Nagel DE, Horan DL, Chandler GL. 2011a. Role of climate and invasive species in structuring trout distributions in the Interior Columbia Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:988–1008.

Wenger SJ, Isaak DJ, Luce CH et al. 2011. Flow regime, temperature, and biotic inter- actions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* **108**:14175– 14180.

Wetzel RG. 2001. *Limnology: Lake and river ecosystems*. 3d ed. San Diego, CA: Academic Press

Whitehead PG, Wilby RL, Battarbee RW, Kernan M, Wade AJ. 2009. A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal* **54**:101–123

Wijnhoven S, Riel MC Van, Velde G Van Der. 2003. Exotic and indigenous freshwater gammarid species : physiological tolerance to water temperature in relation to ionic content of the water. *Aquatic Ecology* **37**:151–158

Wolanski E, Boorman, LA, Chı´charo L, Langlois-Saliou E, Lara R, Plater AJ, Uncles RJ, Zalewski M, 2004. Ecohydrology as a new tool for sustainable management of estuaries and coastal waters. *Wetlands Ecology and Management* **12**: 235 -276

Woodward G, Dybkjaer JB, Ólafsson JS, Gíslason GM, Hannesdóttir ER, Friberg N. 2010b. Sentinel systems on the razor's edge: effects of warming on Arctic geothermal stream ecosystems. *Global Change Biology* **16**(7): 1979-1991

Woodward G, Perkins DM, Brown LE. 2010a. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1549): 2093–2106.

Woodward G, Brown LE, Edwards FK, Hudson LN, Milner AM, Reuman DC, et al. 2012. Climate change impacts in multispecies systems: drought alters food web size structure in a field experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**:2990– 2997.

Wooster DE, Miller SW, Debano SJ. 2012. An examination of the impact of multiple disturbances on a river system : Taxonomic metrics versus biological traits. *River Research and Applications* **28**: 1630–1643.

Xin Z, Kinouchi T. 2013. Analysis of stream temperature and heat budget in an urban river under strong anthropogenic influences. *Journal of Hydrology* **489**: 16–25.

Yang DQ, Liu BZ, Ye BS. 2005. Stream temperature changes over Lena River basin in Siberia. *Geophysical Research Letters* **32**(5): 101-123.

Young RG, Huryn AD. 1996. Inter-annual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 2199–2211.

Yue S, Pilon P, Phinney B, Cavadias G. 2002. The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrological Processes* **16**: 1807-1829.

Zebisch M, Grothmann T, Schröter D, Hasse C, Fritsch U. 2005. *Climate change in Germany: vulnerability and adaptation of climate sensitive sectors*. Environmental research of the federal ministry of the environment, Nature conservation and nuclear safety, Research Report 201 41 253, UBA-FB 000844/e. Available from: www.umweltbundesamt.de/sites/default/files/medien/publikation/long/2974.pdf

Statement of academic integrity

I hereby certify that the submitted thesis "*River temperature behaviour in changing environments: trends, patterns at different spatial and temporal scales and role as a stresso*r" is my own work, and that all published or other sources of material consulted in its preparation have been indicated. All collaboration that has taken place with other researchers is indicated and I have clearly stated my own personal share in those investigations in the Thesis Outline. I confirm that this work has not been submitted to any other university or examining body in an earlier doctoral procedure in the same or a similar form, or has been judged to be insufficient.

Berlin, 15.12.2015

Roshni Arora

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"It always seems impossible until it's done"- Nelson Mandela

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APPENDIX A: Supplementary material for Chapter 2

Figures

Figure SII.1 Boxplots showing significant river temperature (RT) trends for two decades. DS stands for dataset, where DS I (total n=132) are sites analysed for 1985-2010 and DS II (total n=475) are sites analysed for 2000-2010.

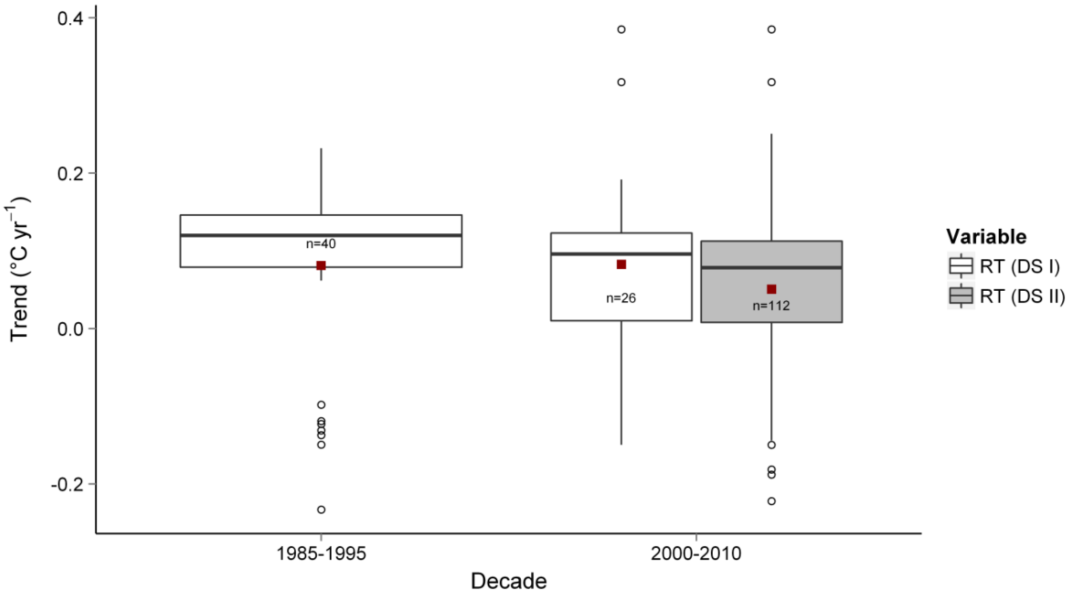


Figure SII.2 Cumulative frequency distribution (ecdf) for proportion of forest, agriculture and urban land use cover types within 1 km^2 site buffers (time period:2000-2010; n=112).

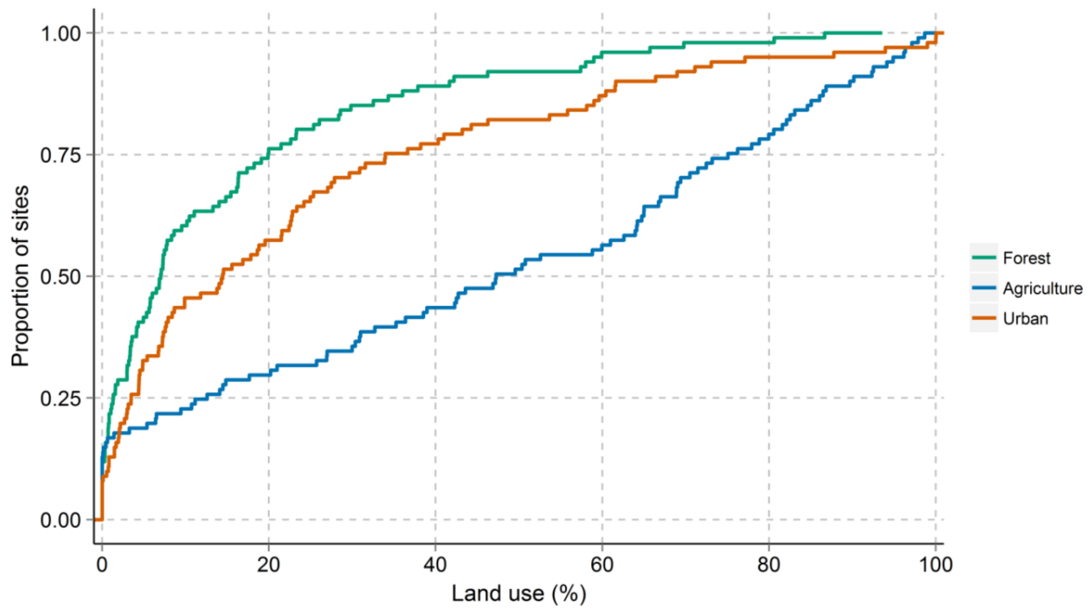


Figure SII.3 Cumulative frequency distribution of significant air temperature (AT)-river temperature (RT) slopes from linear regression for both time periods.

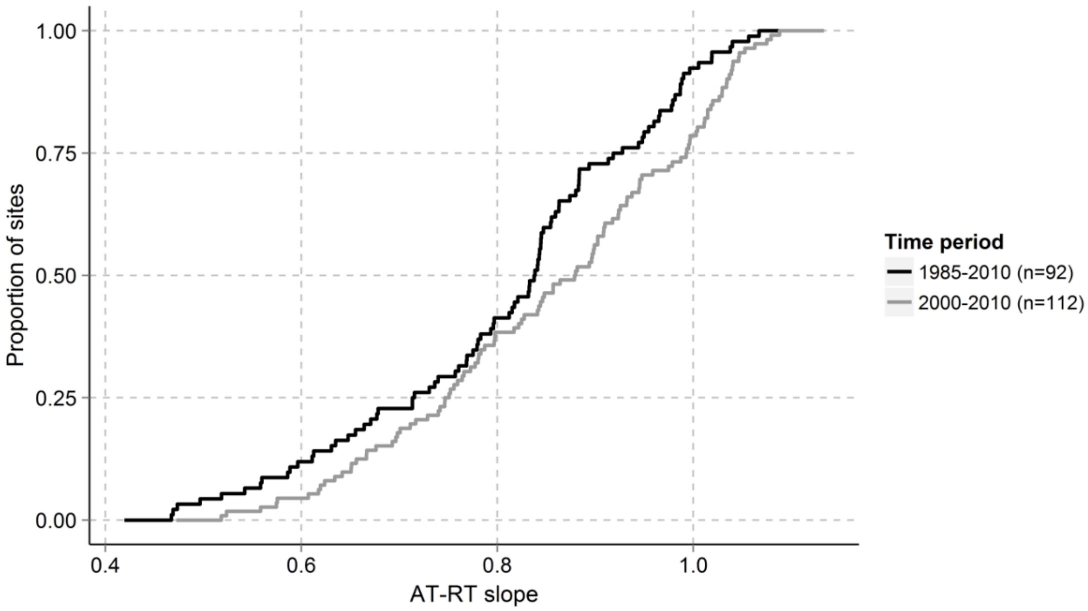
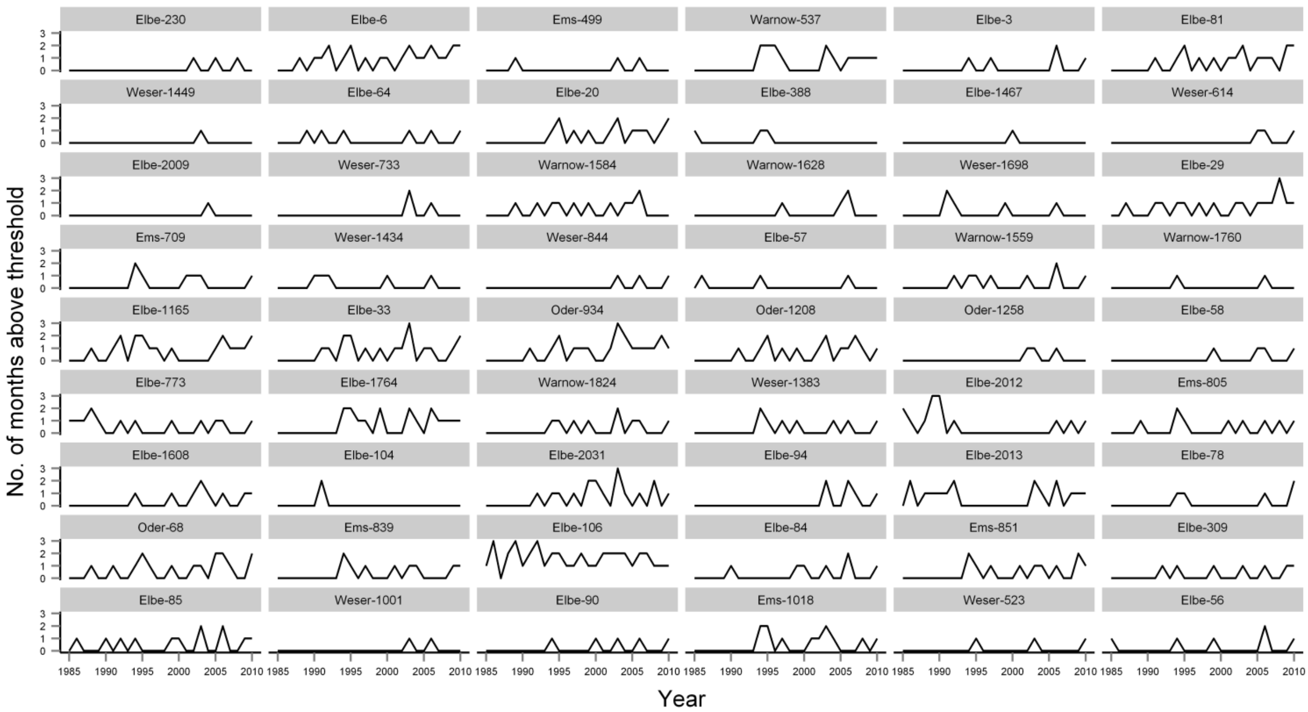


Figure SII.4 Frequency of months with mean monthly river temperature above the threshold temperature of 22°C plotted for several sites. The threshold temperature was based on thermal limits of fish and invertebrate species as mentioned in Hardewig et al. (2004), Haidekker & Hering (2008) and Vornanen et al. (2014).



Tables

Table SII.1 Mean (±S.E.) of significant river temperature trends in the different ecoregions and river types in Germany.

Ecoregion	River type	Number of sites	Mean (±S.E.)
Time period: 1985-2010			
Central highlands	Small fine substrate dominated calcareous highland rivers	4	0.03 (±0.013)
	Small fine substrate dominated siliceous highland rivers	1	0.03
	Mid-sized fine to coarse substrate dominated siliceous highland rivers	1	0.02
	Mid-sized fine to coarse substrate dominated calcareous highland rivers	9	0.02 (±0.015)
	Very large gravel-dominated rivers	1	0.003
	Large highland rivers	14	-0.002 (±0.012)
Central plains	Marshland streams of the coastal plains	3	0.07 (±0.006)
	Very large sand-dominated rivers	5	0.06 (±0.022)
	Small loess and loam-dominated lowland rivers	2	0.05 (±0.023)
	Mid-sized and large sand and loam-dominated lowland rivers	32	0.03 (±0.005)
	Small sand-dominated lowland rivers	2	0.02 (±0.012)
	Backwater and brackish water influenced Baltic Sea tributaries	1	0.01
	Mid-sized and large gravel-dominated lowland rivers	1	0.00
	Small gravel-dominated lowland rivers	2	-0.01 (±0.018)
Ecoregion-independent river types	Mid-sized and large organic substrate-dominated rivers	4	0.05 (±0.015)
	Lake outflows	5	0.04 (±0.020)
	Small streams in riverine floodplains	3	0.03 (±0.022)
Time period: 2000-2010			
Central highlands	Mid-sized fine to coarse substrate dominated siliceous highland rivers	2	0.06 (±0.048)
	Small coarse substrate dominated siliceous highland rivers	1	0.01
	Small fine substrate dominated calcareous highland rivers	2	-0.01 (±0.001)
	Small fine substrate dominated siliceous highland rivers	2	-0.12 (±0.107)

	Mid-sized fine to coarse substrate dominated calcareous highland rivers	2	-0.13 (±0.023)
	Very large gravel-dominated rivers	1	-0.14
	Large highland rivers	3	-0.17 (±0.014)
Central plains	Mid-sized and large sand and loam-dominated lowland rivers	47	0.11 (±0.012)
	Very large sand-dominated rivers	16	0.07 (±0.013)
	Small sand-dominated lowland rivers	9	0.03 (±0.031)
	Small gravel-dominated lowland rivers	2	0.00 (±0.079)
	Marshland streams of the coastal plains	7	-0.02 (±0.041)
	Small loess and loam-dominated lowland rivers	1	-0.11
	Mid-sized and large gravel-dominated lowland rivers	1	-0.14
Ecoregion-independent river types	Lake outflows	6	0.06 (±0.038)
	Mid-sized and large organic substrate-dominated rivers	4	0.05 (±0.023)
	Small streams in riverine floodplains	2	0.04 (±0.038)

Table SII.2. Mean (±S.E.) of river temperature trends shown for the two datasets (DS I and II) used in the study for different time periods. *Decadal analysis for DS I was done at sites with significant river temperature trends during 1985-2010.

Dataset / Time period	**1985-1995**	**2000-2010**	**1985-2010**
All trends			
DS I (n=132)	0.06 (±0.01) (n=92*)	0.025 (±0.01) (n = 92*)	0.019 (±0.003) (n = 132)
DS II (n=475)	----	0.018 (±0.003) (n = 475)	---
All significant trends			
DS I (n=132)	0.08 (±0.01) (n = 40)	0.08 (±0.02) (n = 26)	0.024 (±0.004) (n = 92)
DS II (n=475)	---	0.05 (±0.01) (n = 112)	---
Significant warming trends			
DS I (n=132)	0.13 (±0.006) (n = 33)	0.11 (±0.02) (n = 23)	0.033 (±0.003) (n = 83)
DS II (n=475)	----	0.09 (±0.008) (n = 89)	---

APPENDIX B: Supplementary material for Chapter 3

Figures

Figure SIII.1 Share of cover of different land use types within 50, 100, 500 and 1000 m buffer widths at all sites on River Spree.

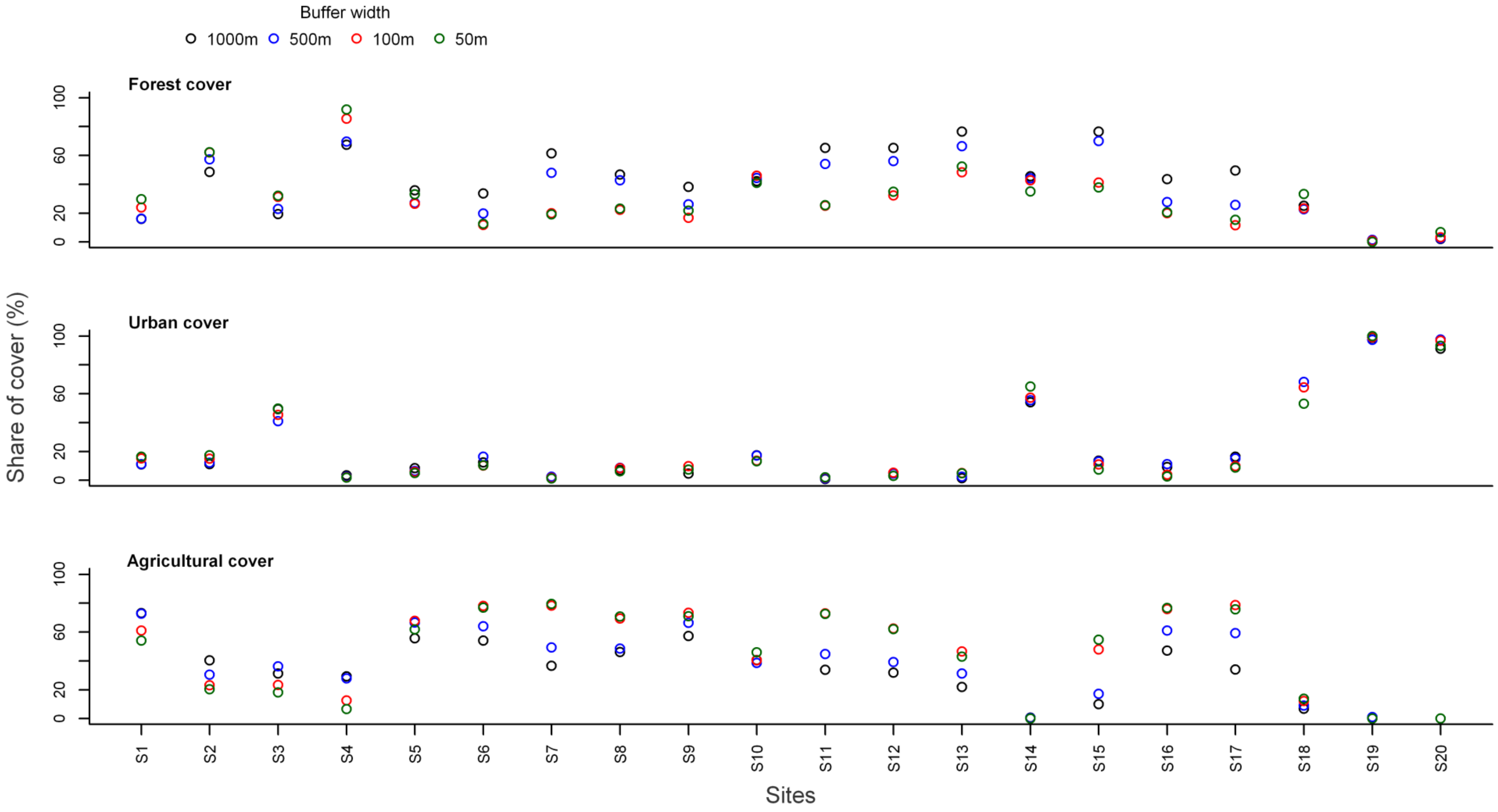


Figure SIII.2 Daily range (maximum-minimum) for the 15th day of each month plotted for 20 sites on River Spree for all months.

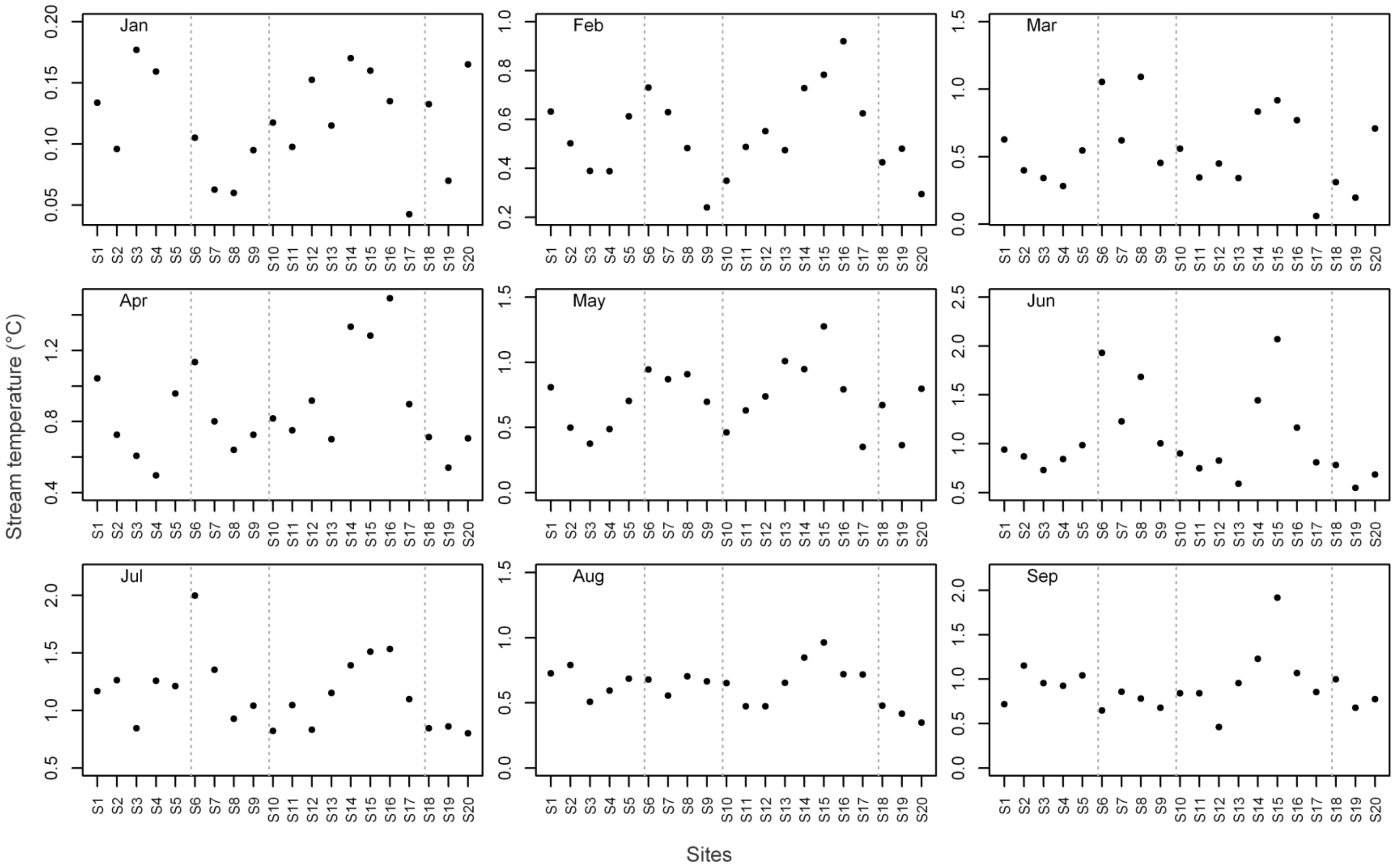
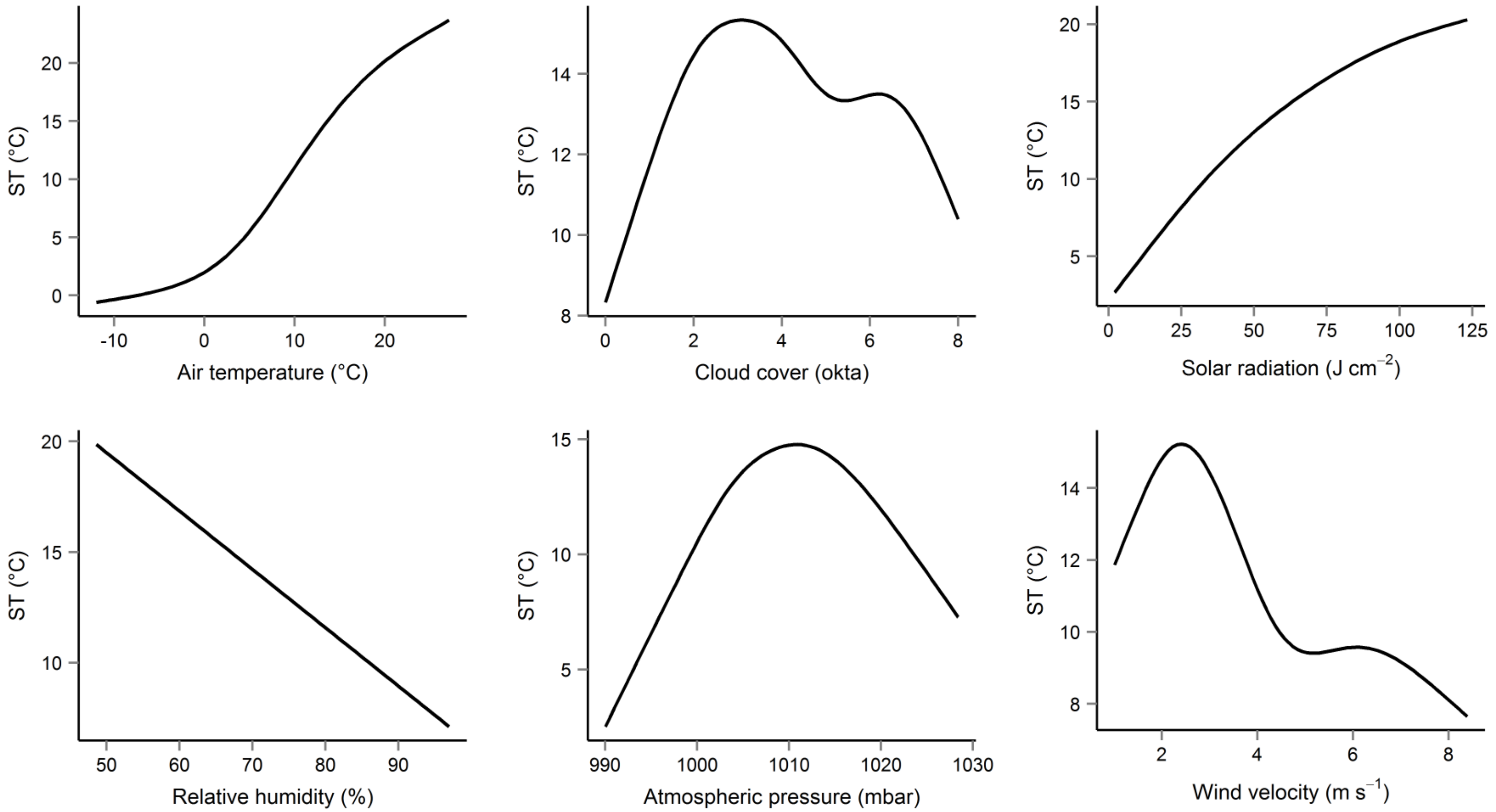


Figure SIII.3 Plots showing the nature of relationship of ST with different atmospheric variables. The curves were determined by the non-linear models using the spline-smoothing function (function gam in mgcv package, R).



APPENDIX C: Heat Flux Equations used in Chapter 3

The following equations are mostly derived from Martin & McCutcheon (1998). Typical values adopted in the analysis are reported within parentheses.

The net thermal energy (E_{atm} ,W m^{-2}) at surface of a water body (without tributary inflow) may be expressed as:

$$E_{atm} = E_s + E_h - E_b - E_e - E_c \, , \tag{1}$$

where E_s= shortwave radiation absorbed, E_h= atmospheric longwave back radiation, E_b = back radiation from water surface, E_e= heat loss due to evaporation, E_c = net heat flux due to sensible heat transfer.

E_s can be calculated as (Imboden and Wüest, 1995):

$$E_s = (1 - r)\, H°s \, (1 - 0.65\, C^2) \, , \tag{2}$$

where r = 0.2, $H°s$ is clear sky solar radiation (W m^{-2}), and C is cloud fraction (-).

E_h can be calculated as:

$$E_h = \alpha \, 0.97 \, \sigma \, (T_a + 273.16)^6 \, (1 + 0.17C) \, , \tag{3}$$

where α is a proportionality constant (0.937 ×10^{-5}), σ is the Stefan-Boltzmann constant (5.67 ×10^{-8} W m^{-2} K^{-4}) and T_a is the air temperature (°C).

E_b can be calculated as:

$$E_b = 0.97 \, \sigma \, (T_w + 273.16)^4 \, , \tag{4}$$

where T_w is the water temperature (°C).

E_e can be calculated as:

$$E_e = \rho \, L_w \, E \, , \tag{5}$$

where

$$E = (a + bW)(es - ea)E_s = (1 - r)\, H°s \, (1 - 0.65\, C^2) \, , \tag{6}$$

$$es = 2.171 \times 10^8 \, e^{(-4157/T_w + 239.09)} \, , \tag{7}$$

$$ea = 2.171 \times 10^{8}\, e^{(-4157/T_d + 239.09)}\,, \tag{8}$$

$$T_d = T_a - ((100 - rh)/5)\,, \tag{9}$$

Here, a (mbar^{-1} m s^{-1}) and b (mbar^{-1}) are wind coefficients with values 1 ×10^{-10} and 1 ×10^{-9} respectively, W is the wind speed (m s^{-1}), E is the rate of evaporation (m s^{-1}), es is the saturated vapour pressure at the water surface temperature (mbar), ea is the vapour pressure at the air temperature (mbar), L_w is the latent heat of evaporation (2.4 ×10^{6} J kg^{-1}), ρ is the density of water (997 kg m^{-3}), T_d is the dew point temperature (°C), and rh is the relative humidity (%).

E_c can be calculated as:

$$E_c = \rho\, L_w\, (a + bW)\, C_b\, (P_a/P)\, (T_w - T_a)\,, \tag{10}$$

where C_b is the Bowen's ratio (0.61 mbar °C^{-1}), P_a is the atmospheric pressure (mbar), and P is the reference pressure at mean sea level (1005 mbar).