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Master Thesis

The effects of altered sediment regimes on Brown Trout *Salmo trutta* and their diet

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Summary

Fluvial ecosystems are highly dynamic, with spatio-temporal fluctuations mainly driven by the sediment and flow regime. Over the last centuries humans have spent much effort taming and exploiting river systems for their benefit and interests. The anthropogenic exploitation, such as channelization or hydropower production, has considerably altered river ecosystems, including their sediment regime. The aim of the present study was to better understand the effects of altered sediment regimes on brown trout *Salmo trutta* and their diet. We studied two groups of alpine streams with a near-natural and a depleted sediment regime, respectively. Study reaches were sampled by quantitative electrofishing and kick-netting. Biotic variables on the population level were measured, such as trout biomass and densities, and macroinvertebrate community composition, as well as on the level of the individual fish (Fulton's body condition factor, stomach contents, food electivity indices). To further assess the impact of sediment alteration selected abiotic variables were measured (Pfankuch stability index, d90 of sediment, CPOM, FPOM, degree on inner clogging). The relationship between abiotic and biotic variables was analysed through stepwise linear regression (linear models and linear mixed models).

We hypothesized that (i) particulate organic matter content in the sediment is generally higher in sediment-depleted streams as compared to streams with a near natural sediment regime, and (ii) trout in streams with a near-natural sediment regime show higher proportions of terrestrial invertebrates in their diet than trout in sediment-depleted streams.

Our categorical variable (near-natural vs. depleted) proved to be an unsuitable descriptor for the pronounced variability observed in the study reaches, both for the biotic and the abiotic variables and on the two hierarchical levels. However, hydromorphological characteristics such as the physical stability of a reach or the particulate organic matter content in the sediment showed complex, but significant influence on brown trout and their diet, also through linkage of different trophic levels.

This study described the relationships between selected abiotic variables that are influenced by sediment alterations and the structure and function of aquatic communities. The results contribute to a better understanding of the high complexity in dynamic fluvial systems and hence to the protection and restoration of these valuable ecosystems and the services they provide.

1. Introduction

Rivers and streams are highly dynamic ecosystems (Power, 2001). Dynamics are mainly driven by flow and sediment regimes (Wohl, 2012) that create vast spatial heterogeneity with often impressively rapid temporal fluctuations (Power, 2001). Considerable changes in discharge occur frequently such as minor floods (Poff et al., 1997). Floods represent disturbances, as defined by Sousa (1984); their influence on the ecosystem is manifold, e.g. as a driver for local food web function and causing substantial changes in the sediment regime (Power, 2001). Such a change might be the wash-out of fine sediments from gravel banks, thereby creating suitable spawning habitats for salmonids and other lithophilic fish (Poff et al., 1997). The brown trout S*almo trutta*, for instance, strongly depends on unclogged, well-oxygenated gravel beds for spawning and egg development (Scheurer et al., 2009). Apart from spawning, sediment dynamics and substrate composition matter throughout the life cycle of *S. trutta*. The initial dispersal of the emerging fry from the gravel is very limited and therefore unclogged gravel beds also serve as nursery habitats (Armstrong et al., 2003). The different gravel sizes in alpine streambeds offer refuge and shelter for young fish (Scheurer et al., 2009). Boulders and substrate heterogeneity increase the diversity of habitat and provide visual isolation and protective cover for juvenile and adult fish (Armstrong et al., 2003). Furthermore brown trout spend much time foraging in the sediment as it also provides habitat for a wide range of macroinvertebrates (Bridcut, 2000; Gowan et al., 2002).

Over the last centuries humans have spent much effort taming and modifying rivers for power generation, flood protection, transportation, water supply and agriculture (Poff et al., 1997; Scheurer et al., 2009). Reservoirs and dams trap all but fine sediments (Poff et al., 1997; Vorosmarty et al., 2003) which can lead to clogging of the downstream river bed and degradation of fish habitats (Sternecker, 2013). Sediment trapping at dams, gravel mining and other land use activities that reduce sediment input ('sediment depletion') can lead to sediment starved flows (Poff et al., 2007) resulting in increased erosion rates and subsequent channel incision (Kemp et al., 2011; Kondolf, 1997; Scheurer et al., 2009). Water abstraction on the other hand reduces erosion rates and the sediment transport within a riparian system (Arroita et al., 2015). In summary, all these anthropogenic impacts reduce physical diversity and connectivity of river systems and cause a reduction in biodiversity (Wohl, 2012). Taking into account the present conditions in a great part of global river systems (Vorosmarty et al., 2003) and in Swiss rivers (Schälchli et al., 2002), high priority should be placed on better understanding the effects of changed sediment regimes on the structure and function of aquatic ecosystems and the services they provide. Improved understanding of ecosystem functioning gives us the possibility

to manage ecosystems more efficiently and making a further step towards a sustainable use of ecosystem services.

The present thesis was part of an interdisciplinary project investigating the ecological effects of sediment depletion in river systems and developing and evaluating measures for sediment rehabilitation. Specifically, this study described the relationships between selected abiotic variables that are influenced by sediment alterations and the structure and function of aquatic communities. In a multi-site field study I surveyed several hydromorphological variables to characterise the abiotic environment and sampled organisms from the upper trophic levels for structural and functional analysis. The study was designed as a two group study system, the first group representing the streams with a near natural sediment regime, while the second group was affected by sediment depletion.

My hypotheses were:

(1) Due to a reduced movement of the streambed, sediment-depleted streams have a higher particulate organic matter content in the sediment than streams with a near-natural sediment regime.

(2) Due to lower organic matter contents in the streambed, trout in streams with a near-natural sediment regime show higher proportions of terrestrial invertebrates in their diet than trout in sediment-depleted streams.

2. Materials and Methods

2.1. Study reach selection

We selected our study reaches in ten alpine streams in the canton Graubünden, which is located in the eastern, alpine part of Switzerland (Figure 1). Information on sediment integrity was retrieved from a cantonal report (unpublished data, Canton Graubünden); data concerning the flow regime and catchment size were gathered from the hydrological atlas (Spreafico et al., 1992). Five study reaches in streams with a near-natural sediment regime were chosen, namely in Val da Camp, Averserrhein in Cresta, Rein da Cristallina, Landquart and Flem. The five study reaches in streams with a depleted sediment regime were in Rein da Medel, Schmuèr, Julia, Spöl and Averserrhein in Innerferrara. Table 1 lists the anthropogenic alterations in the catchment upstream the study reaches which have an impact on the sediment regime of the stream. For methodological reasons, all study reaches had to be wadable.
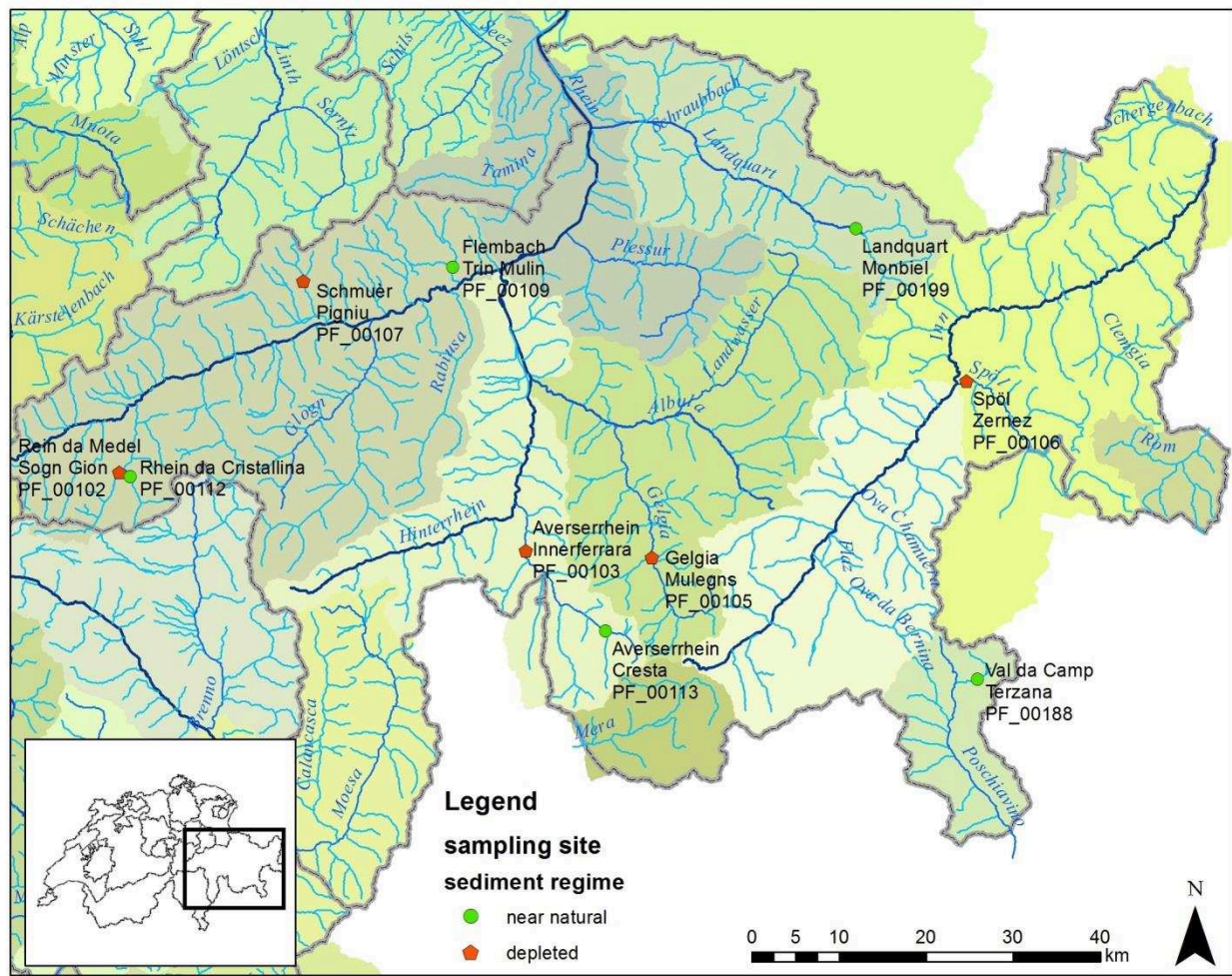

Figure 1: The ten study reaches. Five near-natural reaches (in green) and five depleted reaches (in red).

Table 1: Characteristics of the catchment upstream the study reaches

	Study reach (coord., lat/long)	Catchment area [km^2]	Dams [1]	Morphology of the banks [2] [km]	Artificial barriers	Water abstractions (>50% of flow)	Diverted flow power stations
near-natural	Rein da Cristallina (46.619/8.844)	27.9	0	No records	0	2	0
	Val da Camp (46.387/10.104)	31.8	0	1: 1.4 2: 0.8 3: 0.5	0	0	0
	Averserrhein, Cresta (46.448/9.550)	41.1	0	1: 39.8 2: 20.5 3: 1.0	0	0	0
	Flem (46.829/9.334)	41.7	0	1: 12.8 2: 19.7 3: 1.0 4: 5.6 5: 0.9	20	2	4
	Landquart (46.856/9.943)	101	0	1: 4.0 2: 9.7 5: 0.2	2	0	0
depleted	Schmuèr (46.818/9.110)	29.6	1 GD	1: 46.4 5: 1.6	1	3	0
	Rein da Medel (46.624/8.827)	46.9	1 SAD	1: 17.0 2: 30.0	2	1	0
	Julia (46.523/9.623)	146	1 ED	1: 9.0 2: 0.9 3: 4.8	15	7	1
	Averserrhein, Innerferrara (46.534/ 9.435)	230	2 SAD 1 GD	1: 21.8 2: 10.1 3: 2.8	11	8	1
	Spöl (46.696/10.102)	434	2 SAD	1: 2.9 2: 9.4 5: 0.2	3	2	0

[1] GD: Gravity dam; SAD: Single arch dam; ED: Embankment dam

[2] 1: natural/near-natural; 2: barely impaired; 3: strongly impaired; 4: artificial; 5: in culverts.

2.2. Electrofishing survey and kick-net sampling

Brown trout were caught using backpack equipment (Hans Grassl GmbH, ELT 62II GCV 135, 300/500 V) during October and November 2014. The reaches were fished quantitatively by setting up two stop nets at the upstream and downstream end. Two to three runs were made depending on the amount of caught fish. A maximum of 30 trout per reach were euthanized for later laboratory analysis. The individuals to be euthanized were first anesthetised in a MS-222, tricaine methanesulfonate solution (Acros Organics; 0.5 g diluted in 10 L water) before taking a standardised picture in a Plexiglas cuvette. The fish were then put back several minutes into the first MS-222 solution before placing them into a higher concentrated MS-222 solution. Subsequently standardised pictures of the individuals' left sides, as well as the weight (± 0.1 g) and their standard and total length (± 1 mm) were taken. For preservation, the fish were cut

open laterally and inserted into a 4 % formalin solution. If more than 30 fish were caught they were measured, weighed and a cuvette picture was taken before releasing them.

Kick-net samples (Hauer et al., 2011) were taken to characterise the macroinvertebrate (MIV) community of a fished reach. At five different locations, a D-frame net with a mesh size of 250 µm was held into the direction of the stream flow and the sampler kicked ten times into the gravel. The five sub-samples were combined into one sample per reach. The sample was then transferred into a recipient filled with a 70 % ethanol solution to preserve the invertebrates for laboratory analysis.

2.3. Abiotic variables

Channel stability of the study reaches was visually evaluated using the method described by Pfankuch (1975). Upper banks, lower banks and stream bed features were qualitatively assessed with a total of 15 sub-criteria (e.g. presence of vegetative bank protection, undercutting, rock angularity). Each variable was ranked in a 4-tiered scheme with predefined weights and the scores summed up to obtain the final stability assessment score. The lower the score, the more stable the study reach.

The degree of inner clogging was determined using the visual classification described by Schälchli et al. (2002). At three locations per reach the composition of the subsurface layer was classified into one of five classes, with the fifth class representing the highest degree of clogging.

The distribution of grain sizes within a study reach was assessed using the pebble count method described by Wolman (1954). The b-axis of a total of 100 stones per reach was measured if grain size was >2 mm; otherwise grain size was indicated as <2 mm. Stones were picked from the tip of the toe at each footstep either along a transect (larger streams and rivers) or following a zig-zag line (streams). Based on these data, the d90-value was determined. d90 is a characteristic parameter describing the grain size distribution converted from a count-based to a quasi-volume distribution following the formula of Fehr (1987). In other words, d90 is the diameter where 90 % of the sediment lies below this size.

To determine the organic matter content of the sediment, three sediment samples were taken within the predominant aquatic habitats of the study reach. First, the surface layer was removed in order to exclude biofilm and macroinvertebrates. The sediment samples were taken at a depth of 10-15 cm with a small shovel and sieved through a 12.5 mm grid into a bucket. The sediment was then transferred into a zip-locked bag and laid on ice before freezing the samples to -20° C in the laboratory. The weight of the collected samples ranged between 0.5 and 1 kg. In the laboratory, the samples were sieved through an 8mm sieve and transferred into 250 ml

aluminium dish. The samples were dried in a freeze dryer (ALPHA 2-4 LDplus, Martin Christ Gefriertrocknungsanlagen GmbH) at -21° C and 0.1 mbar over 20 hours. The freeze-dried samples were divided into a coarse fraction of grains containing coarse particular organic matter (CPOM, 2-8 mm) and a finer fraction containing fine particular organic matter (FPOM, <2 mm) by sieving through a 2 mm sieve. In order to have a suitable volume to combust in a muffle (L9/11, Nabertherm), the fine particular fraction was subsampled into two equal fractions using a riffle splitter (Microsplitter SS-16-3, Carpco Inc.). One of the two subsamples was weighed before combustion at 400° C for four hours. The weight loss after combustion represents the ash-free dry mass (AFDM) of the organic matter in the subsample. The absolute values were then standardised to grams per kilograms of sediment.

2.4. Biotic variables – population level

The estimates for brown trout population densities were calculated using the R package *FSA* developed by Ogle (2012). Biomass was then estimated using the obtained population estimates. They were standardised over the mean weight and population proportion of fish within the four length groups 0-80 mm, 81-160 mm, ,161-240 mm and >240 mm (Schager et al., 2007). The MIV-samples were subsampled in a tray (33x48 cm) that was subdivided in 24 fields (6x11 cm). A minimum number of 300 invertebrates defined the amount of fields that were examined. All the invertebrates found in the examined fields were identified with literature (Jessup et al., 1999; Sundermann et al., 2004; Tachet et al., 2000; Zwick, 2004) to order level. The order of Diptera was further identified into the two suborders Nematocera and Brachycera and the family of Chironomidae within the suborder of Nematocera was also identified if possible.

2.5. Biotic variables – individual level

The index of body condition for all brown trout per reach was determined by the Fulton's condition factor *K*

$$K = \frac{W*10^5}{L^3},$$

where *W* is the weight [g] and *L* the total length of the fish [mm]. The residual values of the linear regression of Fulton's K to the total length were calculated and used for evaluation (Broedersen et al., 2008).

Ten fish per reach were chosen for stomach content analysis. We focused the analysis on fish within the size range of 100 mm to 200 mm total length. If there were not enough fish within the preferred size range, those fish which measured closest to 100 mm were chosen. The stomachs of the ten chosen fish were removed and weighed before and after emptying them in lab. The

contents of the stomachs were transferred into falcon tubes with 70 % ethanol to preserve them until identification. The stomach fullness [%] was determined by dividing the weight of the content by the weight of the fish and multiplied by 100 (Smyly, 1952). The stomach contents (SC) were later identified and quantified with literature in the laboratory (Jessup et al., 1999; Sundermann et al., 2004; Tachet et al., 2000). To ensure comparability of the invertebrate data the overall proportions of each invertebrate taxa were calculated. The proportions for Ephemeroptera, Plecoptera and Trichoptera were also summed up and given as one proportion (SC_ept).

To quantify positive or negative food selection of fish we calculated the modified electivity index or relative difference *D* (Jacobs, 1974) for each food source and fish with the formula:

$$D = \frac{r-p}{r+p-2rp},$$

where *r* is the proportion of a given food type in the stomach (e.g. SC_ept; [0 to 1]) and *p* is the proportion of the same food type in the environment [0 to 1], i.e. the kick-net sample of the reach where the fish was caught (e.g. MIV_ept).

2.6. Statistical analysis

Statistical analyses were performed using R software version 3.1.1. (Team, 2014). In a first step of analysis, independent samples t-tests were conducted to test for differences between the two sediment regime groups for all abiotic and for the biotic variables available on the population-level. In order to investigate the relationship between the abiotic and biotic variables, linear models were fitted for biotic response variables on population level and linear mixed models for biotic response variables on the level of the individual fish using the R package *arm* (Gelman et al., 2015). For both linear and linear mixed models an automated stepwise model selection was performed using the function *dredge* and *get.models* package *MuMIn* (Barton et al., 2015) choosing the models with lowest Akaike Information Criterion (AIC). Abiotic variables included were Pfankuch stability index, d90, CPOM, FPOM, degree on inner clogging and catchment area.

The statistical parameters of linear and linear mixed models are expressed as effect size, standard error, and adjusted R^2 and conditional R^2, respectively, as described by Nakagawa et al. (2007) and Nakagawa et al. (2013). For the mixed models the significance of the abiotic variables are derived from the normed confidence intervals of the effect sizes. The strength of the effect size considered to be small for values between 0.1 and 0.3, medium for values between 0.3 and 0.5 and strong for values above 0.5 as described by Nakagawa et al. (2007).

3. Results

3.1. Descriptive statistics

3.1.1. Abiotic variables

Pronounced variability between study reaches was found for all abiotic variables considered. Figure 2 shows the Pfankuch stability indices estimated in each reach. The Spöl had the highest overall index and the highest stream bed index, with a score of 99 and 53, respectively. The highest lower bank index was observed in the Averserrhein in Cresta (33), whereas the Schmuèr had the highest upper bank index (26). Fine particulate matter concentration (FPOM) was highest in Val da Camp (2.1 g/kg; Figure 3), whereas the highest CPOM concentrations were found in the Julia (2.4 g/kg). Generally, a low degree of clogging was found (Figure 4), except for the Flem, with a median of four. In the Julia, the calculated d90 of the sediment was 1'390 mm (Figure 5), representing the highest value, whereas a minimum d90 of 49 mm was reached in the Spöl. Near-natural reaches showed steeper grain size distribution curves, whereas depleted reaches showed a flattened curve behaviour, resulting in higher d90 values.
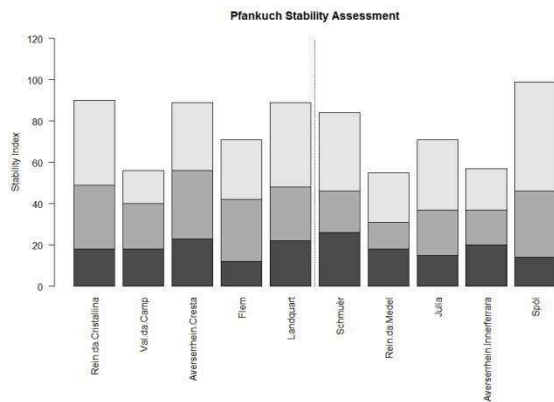

Figure 2: Pfankuch Stability Index. Reaches with a near natural sediment regime are shown on the left, sediment-depleted reaches on the right. *light grey*: stream bed, *grey*: lower banks, *dark grey*: upper banks.
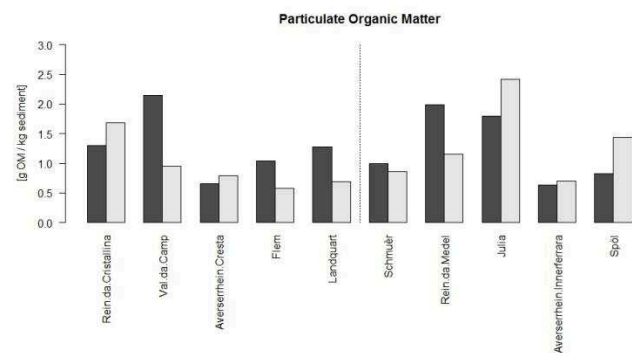

Figure 3: Particulate organic matter. Reaches with a near natural sediment regime are shown on the left, sediment-depleted reaches on the right. *dark grey*: FPOM. *light grey*: CPOM.
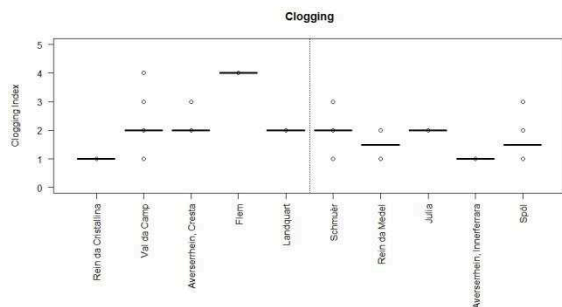

Figure 4: Degree of inner clogging. Bars represent medians**.** Reaches with a near-natural sediment regime are shown on the left, sediment-depleted reaches on the right.
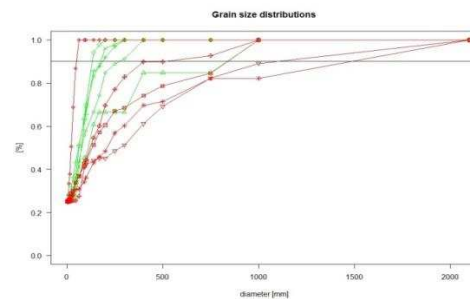

Figure 5: Grain size distribution curves. Reaches with a near-natural sediment regime are shown in *green*, sediment-depleted reaches in *red*. The horizontal line indicates d90 values.

3.1.2. Biotic variables – population level

Biotic variables measured on the population level varied widely across study reaches. The Julia showed the highest estimated population densities with 4'680 individuals/ha (Figure 6) and also the widest confidence intervals (±2'266). In contrast, a minimum density of 465 individuals/ha was estimated for Averserrhein in Cresta. The highest brown trout biomass of 150.9 kg/ha was also found in the Julia (Figure 7).

Figure 8 shows the macroinvertebrate (MIV) proportions of all identified taxa for the two sediment type groups as gathered in the kick-net samples. The variability of the proportions was higher for all invertebrates in near-natural than in depleted reaches, except for Plecoptera and Trichoptera.
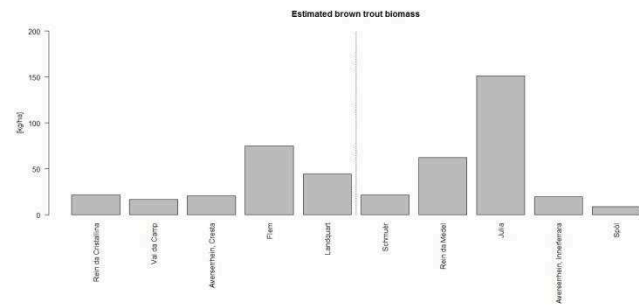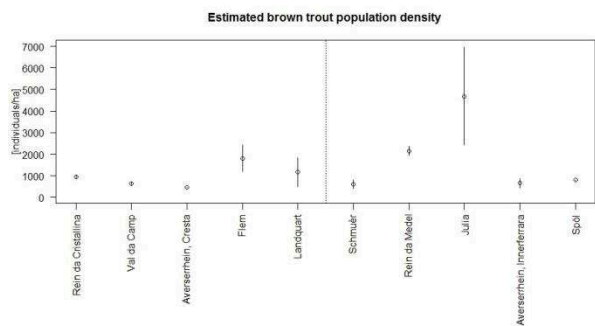

Figure 6: Estimated trout population densities per hectare. Reaches with a near-natural sediment regime are shown on the left, sediment-depleted reaches on the right. Whiskers represent 95% confidence intervals.

Figure 7: Estimated biomass per hectare. Reaches with a near-natural sediment regime are shown on the left, sediment-depleted reaches on the right.
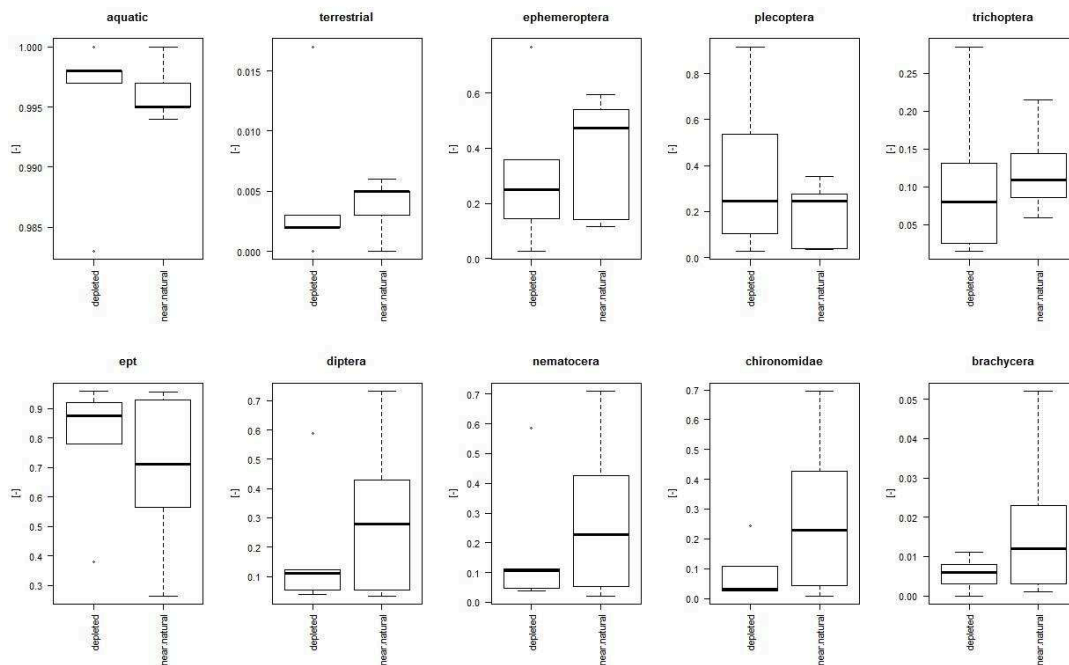

Figure 8: MIV proportions for the two sediment regime groups, separated by taxonomic groups. Individual plots have different scaling of y-axis.

3.1.3. Biotic variables – individual level

All measured biotic variables showed high variability across the reaches, except for stomach fullness (e.g. low variability in Val da Camp vs. high in Averserrhein in Innerferrara; Figure 9). The overall ept proportions of stomach contents (SC_ept) varied considerably over the whole range from 0 to 1 (Figure 10). While ept proportions in some streams had very small variability (e.g. Averserrhein Cresta), ept proportions in other streams such as Flem were very variable. Electivity indices for ept taxa were all negative except for the reaches Flem and Landquart (Figure 11). The electivity indices for aquatic invertebrates all showed pronounced within-population variability except for single streams such as Flem, where the electivity indices of all ten fish were 1, 0 or -1, respectively (Figure 12). K residual values were very similar throughout the different streams although in some streams they were slightly negative and in others showed positive trends (Figure 13).
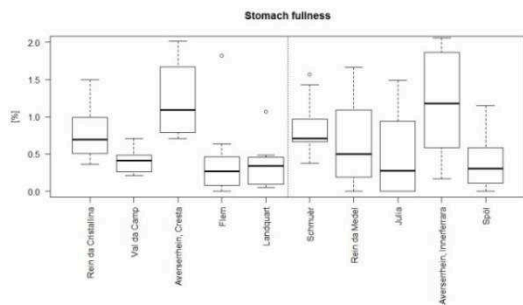

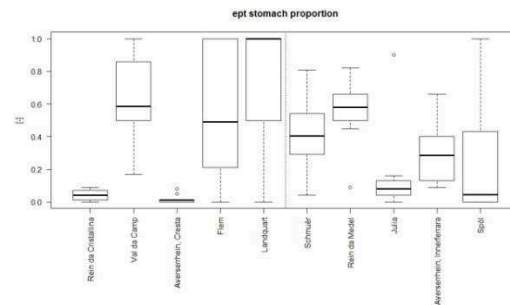**Figure 9:** Stomach fullness. *n*=10 fish per reach.

Figure 10: ept proportions of stomach contents; *n*=10 fish per reach.
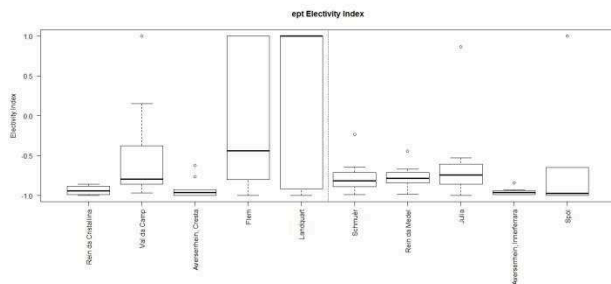

Figure 11: Electivity Indices D for ept taxa. *n*=10 fish per reach.
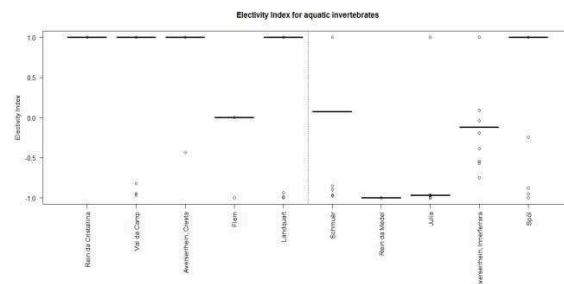

Figure 12: Electivity Indices D for aquatic invertebrates. *n*=10 fish per reach, all individual data points and medians shown.
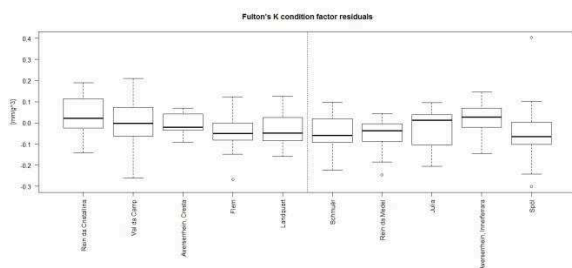

Figure 13: Residual values of linear regression of K as a function of total length for Fulton's K condition factor. *n*=10 fish per reach.

3.2. Statistical tests

3.2.1. t-Tests

No significant differences were observed neither for the measured biotic variables on population level, nor for the abiotic variables (data not shown).

3.2.2. Linear Models – population level

Abiotic variables that did significantly contribute to the model are marked with asterisks in Table 2. Abiotic variables that were not included in the model did not contribute to the explanation of variance of the biotic variable and were excluded from Table 2. No significant interactions between abiotic variables were found.

Trout biomass and population density were significantly positively correlated with CPOM and clogging. MIV-terrestrial was significantly positively correlated with catchment area, whereas MIV-aquatic correlated positively, but not significantly with d90. MIV-Brachycera was significantly positively correlated with clogging and significantly negatively with d90.

No relations between MIV-Chironomidae and abiotic variables were found (data not shown).

Table 2: Stepwise model selection (linear models) for variables on population level. MIV = macroinvertebrates from kick-net sampling. Significance levels (2-tailed): '***'<0.001, '**' < 0.01, '*' < 0.05

Biotic variable	Abiotic variables	Effect size	Std. Error	Adj. R^2
biomass	CPOM*	0.604	0.24	0.5470
	clogging*	0.761	0.24	0.5470
population density	CPOM*	0.604	0.24	0.5470
	clogging*	0.761	0.24	0.5470
MIV-terrestrial	catchment area**	0.805	0.21	0.6036
MIV-aquatic	d90	0.613	0.28	0.2979
MIV-Brachycera	d90*	-0.309	0.13	0.8600
	clogging***	0.863	0.13	0.8600

3.2.3. Linear Mixed Models – individual level

No significant interactions between abiotic variables were found. Abiotic variables that were not included in the model did not contribute to the explanation of variance of the biotic variable and were excluded from Table 3. No relationship between the following biotic variables and abiotic variables were found: K, SC-fullness, SC-aquatic, SC-Diptera, SC-Nematocera, SC-Brachycera, D-Nematocera and D-Chironomidae (data not shown).

All of the correlations in Table 3 were significant. Whereas SC-ept was negatively correlated with CPOM with a medium effect and with FPOM with a strong positive effect, SC-terrestrial showed a positive relationship with CPOM, with a medium effect. D-terrestrial was correlated to sediment type and Pfankuch with medium effects (both negative). D-aquatic was positively correlated with Pfankuch with a medium effect. D-ept and D-Diptera showed a positive relationship with clogging. D-Brachycera were negatively correlated to clogging and Pfankuch with a medium effect and to FPOM with a weak effect.

Table 3: Stepwise model selection (linear mixed models) for variables on individual level. SC = stomach contents, D = electivity index. Significance levels (2-tailed): '***'<0.001, '**' < 0.01, '*' < 0.05

Biotic variable	Abiotic variable(s)	Effect size	Std. Error	Cond. R^2
SC-terrestrial	CPOM*	0.355	0.11	0.2311
SC-ept	FPOM*	0.457	0.16	0.4696
	CPOM*	-0.506	0.16	0.4696
D-terrestrial	sediment type*	-0.303	0.12	0.3710
	Pfankuch*	-0.392	0.12	0.3710
D-aquatic	Pfankuch*	0.392	0.16	0.3343
D-ept	clogging*	0.358	0.16	0.3856
D-Diptera	clogging*	-0.374	0.17	0.4257
D-Brachycera	clogging*	-0.311	0.09	0.2427
	Pfankuch*	-0.453	0.11	0.2427
	FPOM*	-0.276	0.11	0.2427

4. <u>Discussion</u>

In the present chapter the validity of the study design is discussed, model results and underlying mechanisms are interpreted, and strengths and weaknesses of methods and data are identified. I close with an outlook on future steps in this field of research.

4.1. Study design

Based on available data on sediment alteration and ecomorphological status of streams (chapter 2.1.), study reaches were attributed to two sediment groups (near-natural vs. depleted). This categorical approach allowed us to treat sediment alteration as a single explanatory variable and to evaluate the significance and explanatory power of earlier assessments.

However, the categorical variable proved to be an unsuitable descriptor for the variability observed in the study reaches, both for the biotic and the abiotic variables. Our two hypotheses had to be rejected. This finding might have different reasons. One reason could be that there really was no effect, i.e. the variables measured were not influenced by sediment alteration. Another reason might be that the sample size was too small and that the effects could therefore not be proven (see chapter 4.3.). Third, the group approach in a multi-site field study might over-simplify the problem, meaning that the real interactions are much more complex. Quantitative, continuous data would be needed for an in-depth analysis. In order to be able to quantify the human impact on the sediment regime, the sediment budget driven by sediment yield and transport capacity in the channel would have to be measured or modelled. To do this, interdisciplinary collaboration with geomorphologists and river engineers is needed.

4.2. Interplay between abiotic and biotic variables

In the present study, various variables were studied on different hierarchical levels (population level vs. individual level). The conceptual model in Figure 14 serves as basis to structure the discussion. The model includes all variables, except for the sediment regime type which proved to be an insufficient descriptor of the observed patterns in abiotic and biotic variables (see chapter 4.1.).
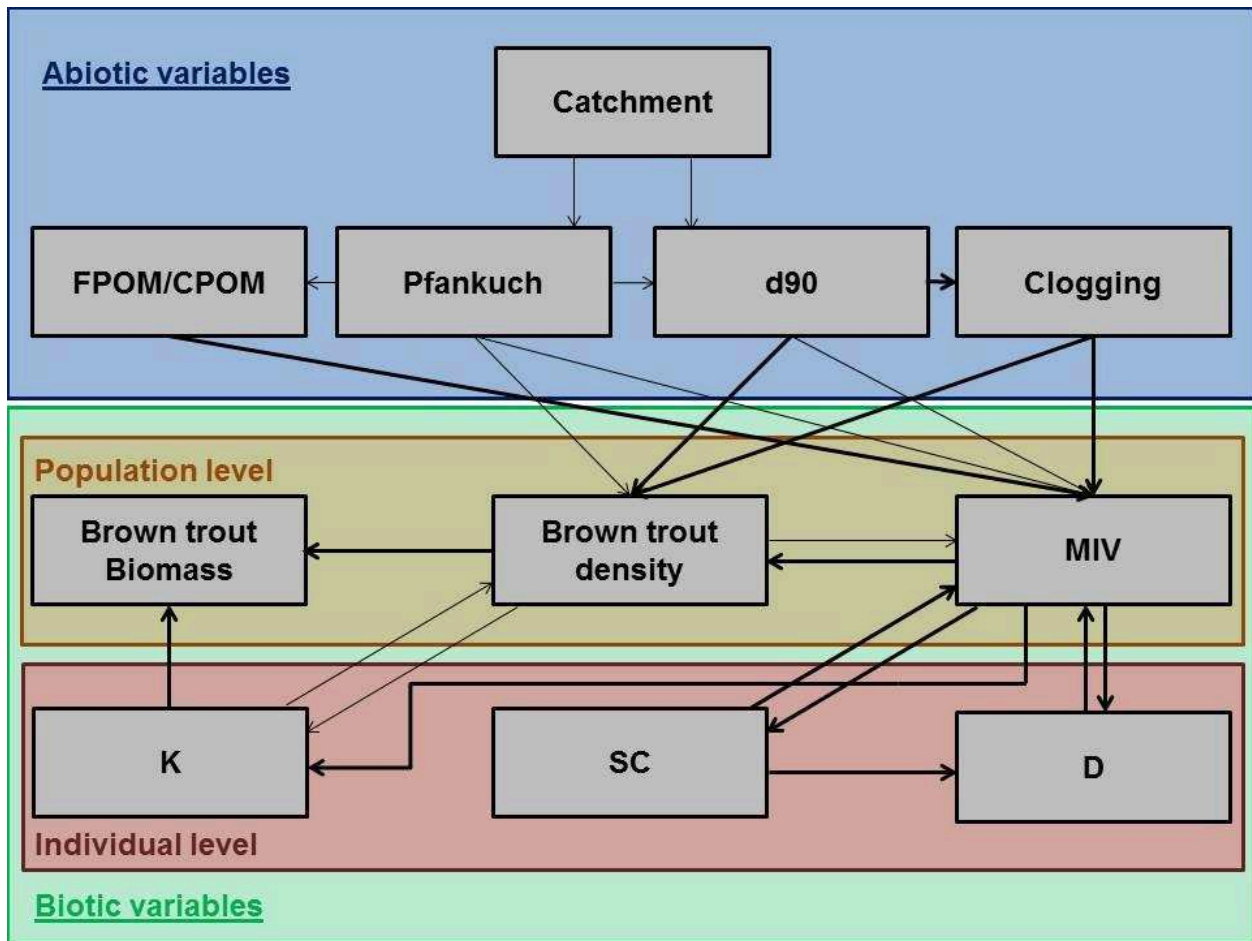
Figure 14: Conceptual model showing expected relationships between abiotic and biotic variables. Bold lines: Relationships expected to be strong. MIV = macroinvertebrates from kick-net sampling, K = Fulton's Condition Factor, SC = stomach contents, D = electivity index.

4.2.1. Population level

Trout biomass and population densities were positively correlated with clogging and CPOM. The former was rather surprising, given that sediment clogging can lower oxygenation and impair the development of salmonid eggs (Bona et al., 2015; Kondolf et al., 2008; Soulsby et al., 2001), potentially resulting in lower trout densities and biomass. However, clogging and organic matter content are expected to rise hand in hand, and up to a certain degree might have a potential beneficial effect on fish biomass because of higher productivity in the system (see below). Stronger clogging reduces interstitial pore space (Descloux et al., 2010; Frostick et al., 1984). Macroinvertebrate highly depend on this pore space for protection against predation (Brusven et al., 1981). Macroinvertebrates in moderately clogged sediment, as found in our study reaches might therefore be more exposed and an easier prey for fish. To separate the effects of clogging and organic matter content an experimental study design that controls for both variables might be of interest.

The positive correlation of CPOM on trout biomass and population densities could be explained through the linkage of trophic levels as described by McCormick et al. (1994) and Power (2001). CPOM serves as food resource for many primary consumers. Higher particulate organic matter contents in resource-limited ecosystems and hence bottom-up controlled food webs would fuel not only primary consumers, but also predatory macroinvertebrates. Higher macroinvertebrate densities then again lead to higher trout population densities and thus higher biomass within a reach. We assume the correlation between clogging and CPOM to be positive, i.e. the higher the clogging the higher the CPOM contents.

The catchment area was positively correlated with the proportions of terrestrial macroinvertebrates found in the kick samples. This observation could result from a combined effect of river size and altitude. Lateral connectivity increases together with the amount of forested riparian areas as rive size tends to be larger below the treeline. These riparian habitats support a wider range of ecological niches (Kawaguchi et al., 2001; Mason et al., 1982) potentially leading to a higher abundance of invertebrates and increased level of terrestrial subsides.

The proportion of aquatic macroinvertebrates in the kick-net samples was positively correlated with d90, but the model fit was quite poor (adjusted R^2 of 0.3) . The reason for this might be that a smooth gradient of grain sizes provides more suitable habitat and better protection from the water current (Power, 2001). However, the model of MIV-Brachycera negatively correlated with the d90 and positively correlated with sediment clogging. These correlations challenge the expected relationship of the abiotic variables on MIV. Further clarification could be achieved by a functional approach, rather looking at biological traits and functional diversity than taxa (Lange et al. 2014).The larvae of Brachycera could be better adapted to fast-flowing environments and clogged interstitial spaces and therefore occupy this ecological niche.

4.2.2.Individual level

CPOM and FPOM, respectively, explained a decent part of the variation (conditional R^2 = 0.23) found in terrestrial invertebrate proportions in trout stomachs, but also for ept-taxa (conditional R^2 = 0.47). While FPOM was positively correlated with the SC-ept proportions, CPOM showed a negative relationship. The latter was against my expectations of linkage between trophic levels. According to Power (2001), I expected that high particulate organic matter could to lead to an increased abundance of primary consumers, as described above, resulting in higher macroinvertebrate abundances and hence to higher ept proportions found in stomachs of trout.

The sediment regime type and the Pfankuch stability index showed a significantly negative relationship with the electivity indices of terrestrial macroinvertebrates. The interpretation of this

result is complicated due to two reasons – a potential sampling bias and the taxonomic composition of kick-net and stomach samples. Terrestrial invertebrates end up in kick-net sampling because they happen to be on the stream bottom or the sample is taken close to the shore. In the stomach contents, however, terrestrial invertebrates most likely represent surface prey, i.e. they were foraged by the fish from the water surface. A higher D-terrestrial does therefore not necessarily mean a stronger selection because the sampling of available food resources in the environment is biased. However, assuming that sampling bias would be constant across reach types, the observation is interesting and would merit future investigations. The electivity indices for ept were positively correlated with clogging whereas the opposite was true for for Diptera. Clogged sediment, as described before represent less available interstitial pore space where macroinvertebrates find shelter (Brusven et al., 1981; Descloux et al., 2010; Frostick et al., 1984). This might explain that fish in higher clogged reaches show higher electivity indices for Ephemeroptera, Plecoptera and Trichoptera larvae because they hide less well in the sediment. The explanation for the Diptera result might be if trout tend to forage disproportionally for Ephemeroptera, Plecoptera and Trichoptera larvae in clogged reaches, Diptera larvae might disproportionally be spared. As Brachycera are the subfamily of Diptera, the explanation to the negative correlation to clogging should also be applicable. The negative correlation of D-Brachycera with the Pfankuch index could be explained through the higher movement of the streambed with higher Pfankuch index values. As habitats become more unstable and harsher, the probability of getting predated is higher and thus the electivity index rises (Power, 2001).

Electivity indices are interesting variables as they allow for analysis of within- and between-population variability. They can give insight into the individual foraging behaviour, which could reflect individual specialisation due to plasticity (Andersson et al., 2006). A shift in resource use on population level could indicate adaptation processes (Andersson et al., 2006; Haas et al., 2010). However, the observed relationship between electivity indices and abiotic variables is an indirect effect and rather the result of a longer cause and effect pathway, thereby complicating the interpretation of the underlying mechanisms.

4.3. Strengths and weaknesses of methods and data

The present master thesis was based on a comprehensive sampling at a limited number of study reaches, i.e. ten reaches in total. Having ten reaches yielded ten values for the variables on the population level to do statistics with. Therefore, analysis and interpretation of the data represent rather an extract than a systematic overview on the ecological effects of sediment depletion. On

the other hand, focusing on ten reaches gave me the opportunity to examine and work with a big variety of different variables, both biotic and abiotic, and covering different levels of the biological hierarchy (population level vs. individual level). This design allowed me to finally relate abiotic variables to biotic variables, with a focus on different trophic levels (e.g. fish, macroinvertebrates).

Concerning the methods used in the field, with hindsight I realised the importance of a decrease in caught fish between the different electrofishing runs. This decrease between runs determines the confidence intervals and thus the precision of the estimates, i.e. it is essential for a precise estimate of population densities. As in the present study the number of runs performed across study reaches varied between two and three, the confidence intervals and thus the precision of the estimates also varied. Consequently making three or more runs depending on the decrease of caught fish between the runs would have reduced confidence intervals and thus given us a more precise estimate.

4.4. Future research

As the results of this study indicate, fluvial systems are highly complex. Much potential lies in future studies within this research field in order to improve our understanding of ecosystem functioning and the ecological effects of altered sediment regimes.

Additional biotic variables that could be considered in future studies are morphometric analyses of individual fish, nutrient levels, algal growth and the analysis of stable isotopes in trout. Studying the morphometry of brown trout would give an insight into how top predators in fluvial systems might respond to sediment alterations (e.g. adaptation, phenotypic plasticity; (Andersson et al., 2006; Haas et al., 2010). As stomach contents can only give us an insight into short-term diet (e.g. a few hours), stable isotope analyses allow to make statements on the long-term diet of trout and the precise and quantified linkage of different trophic levels interacting in the ecosystem (e.g. food chain length, allochthonous vs. autochthonous food sources; (Jardine et al., 2014; Post, 2002). Measurement of nutrient levels and algal growth improve the understanding of trophic dynamics, as algae and cyanobacteria represent the very basis of the food web being the primary producers in riverine systems (McCormick et al., 1994; Power, 2001). Also the data of the individual fish could be looked at in more detail in order to understand how individual differences, for instance in body size, might affect the foraging behaviour.

4.5. Conclusions

Our categorical variable (near-natural vs. depleted) proved to be an unsuitable descriptor for the pronounced variability observed in the study reaches, both for the biotic and the abiotic variables and on the two hierarchical levels. However, hydromorphological characteristics such as the physical stability of a reach or the particulate organic matter content in the sediment showed complex, but significant influence on brown trout and their diet, also through linkage of different trophic levels.

This study described the relationships between selected abiotic variables that are influenced by sediment alterations and the structure and function of aquatic communities. The results contribute to a better understanding of the high complexity in dynamic fluvial systems and hence to the protection and restoration of these valuable ecosystems and the services they provide.

<u>Statement of Authorship</u>

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Alvaro Baumann y Carmona

Kastanienbaum, September 4th 2015

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