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Highlights 26

• Soil moisture, groundwater and ERT data reveal moisture dynamics of a forest strip • Sub-surface moisture dynamics altered within strip but not beyond 15 m downslope Water table depths within the forest are lower than the surrounding grassland Forest strip had no impact on groundwater connectivity during larger storms 27 28 29 30 31 32 33 34 35

Keywords 36

Electrical resistivity tomography (ERT); flooding; forest strip; groundwater; runoff; soil moisture 37 38

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Abstract 40

- Forest cover has a significant effect on hillslope hydrological processes 41
- through its influence on the water balance and flow paths. However, 42

knowledge of how spatial patterns of forest plots control hillslope hydrological 43

- dynamics is still poor. The aim of this study was to examine the impact of an 44
- across-slope forest strip on sub-surface soil moisture and groundwater 45
- dynamics, to give insights into how the structure and orientation of forest 46
- cover influences hillslope hydrology. Soil moisture and groundwater dynamics 47
- were compared on two transects spanning the same elevation on a 9° 48
- hillslope in a temperate UK upland catchment. One transect was located on 49

improved grassland; the other was also on improved grassland but included a 14 m wide strip of 27-year-old mixed forest. Sub-surface moisture dynamics were investigated upslope, underneath and downslope of the forest over 2 years at seasonal and storm event timescales. Continuous data from pointbased soil moisture sensors and piezometers installed at 0.15, 0.6 and 2.5 m depth were combined with seasonal $($ \sim bi-monthly) time-lapse electrical resistivity tomography (ERT) surveys. Significant differences were identified in sub-surface moisture dynamics underneath the forest strip over seasonal timescales: drying of the forest soils was greater, and extended deeper and for longer into the autumn compared to the adjacent grassland soils. Water table levels were also persistently lower in the forest and the forest soils responded less frequently to rainfall events. Downslope of the forest, soil moisture dynamics were similar to those in other grassland areas and no significant differences were observed beyond 15 m downslope, suggesting minimal impact of the forest at shallow depths downslope. Groundwater levels were lower downslope of the forest compared to other grassland areas, but during the wettest conditions there was evidence of upslope-downslope water table connectivity beneath the forest. The results indicate that forest strips in this environment provide only limited additional sub-surface storage of rainfall inputs in flood events after dry conditions in this temperate catchment setting. 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70

1 Introduction 71

There is renewed interest in forest strips (often termed "field boundary planting", "shelterbelts" or "buffer strips") as a flood management tool in wet upland environments (Dadson et al., 2017; Lane, 2017; Soulsby et al., 2017). Past work in the UK has shown that forest shelterbelts in improved grassland can control surface runoff (Wheater et al., 2008; Wheater and Evans, 2009). This work, and other studies, have reported significant increases in soil water storage capacity in shallow soils and increased infiltration rates within forest strips, and evidence of forest rain shadow effects on soil moisture in adjacent grassland (Jackson et al., 2008; Lunka and Patil, 2016; Marshall et al., 2009). Thus understanding the impacts of forest strips on subsurface hydrology appears key for controlling surface runoff and such interventions have the potential for "reducing run-off even when only present as a small proportion of the land cover" (Carroll et al., 2004, p. 357). If these findings can be generalised, there are obvious applications within a catchment management perspective for reducing flood risk. They are also important globally, given rapid changes in land use towards more mosaic landscapes and the effects this might have on hydrological processes (Haddad et al., 2015; Ziegler et al., 2004; Zimmermann et al., 2006). 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89

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While some evidence of forest strip impacts on hillslope hydrology exists, there has been limited mechanistic investigation of forest strip impacts on hillslope runoff processes. Of course, mechanistic studies on single completely forested hillslopes have been conducted for decades (Hewlett and Hibbert, 1967; Tromp-van Meerveld and McDonnell, 2006; Wenninger et al., 2004). But the 'black box' before and after treatments applied at the catchment scale (e.g. Hornbeck et al., 1970; Swank et al., 1988) have not been conducted at 91 92 93 94 95 96 97

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the hillslope scale. At best there are some hillslope intercomparisons 98

(Bachmair and Weiler, 2012; Scherrer et al., 2007; Uchida et al., 2006, 2005) 99

that explore hillslope response under different land covers. All of these 100

approaches suffer from difficulties in controlling for significant heterogeneities 101

even at the plot scale, a reliance on point-based data, and the challenges that 102

these raise for developing transferable process understanding (Bachmair and Weiler, 2012). 103 104

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Therefore, whilst plot scale studies have shown measurable impacts of forest cover on local hydrology, the use and application of these findings to assess the effectiveness of forest strip planting at the hillslope scale is limited. Specifically, forest strip planting raises important additional questions related to the location and structure of forest cover in landscapes and its interaction with other physical hillslope properties. For example, forest strips or vegetation patches in more arid environments appear to 'interrupt' hydraulic connectivity across landscapes (Fu et al., 2009; Liu et al., 2018) so may have variable effects on downslope hydrological processes. However, such questions have only been looked at in a few modelling studies (Reaney et al., 2014). 106 107 108 109 110 111 112 113 114 115 116

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Here we examine the influence of a forest strip on hillslope sub-surface hydrological dynamics. We focus on a typical example of a narrow (14 m wide), mixed forest shelterbelt planted on improved grassland (land used for grazing that has been improved through management practices such as liming or drainage) - a configuration similar to that being used in some 'natural' flood risk management schemes in the UK (Environment Agency, 2018; Tweed Forum, 2019). We pair hillslope scale soil moisture and 118 119 120 121 122 123 124

groundwater level measurements with time-lapse electrical resistivity 125

tomography (ERT) to help extrapolate from point-based measurements to 126

hillslope scale process understanding. We build on work by Cassiani et al. 127

(2012), Garcia-Montiel et al. (2008) and Jayawickreme et al. (2008), extending 128

- the ERT technique to investigate the interaction of two vegetation types and 129
- spatial orientation on the slope. Our specific questions are: 130
- 1. How do across-slope forest strips alter soil moisture and groundwater level dynamics beneath the forest? 131 132
- 2. Do forest strips have downslope impacts on soil moisture and groundwater level dynamics? 133 134
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We consider these questions over seasonal and storm event timescales, and 136

also the potential implications from a flood risk management perspective. 137

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2 Methods 139

2.1 Site description 140

The experiment was established on a hillslope in the 67 km² Eddleston Water catchment, a tributary of the River Tweed in the Scottish Borders, UK (Figure 1). The catchment hosts an ongoing project initiated in 2010 to investigate the impact of natural flood management (NFM) measures aimed at controlling runoff from farmland and forest land (Werritty et al., 2010). The measures include tree-planting, establishment of holding ponds on farmland, remeandering the Eddleston Water river, and the construction of 'leaky' dams in 141 142 143 144 145 146 147

some sub-catchments (Tweed Forum, 2019). 148

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- Catchment characteristics are typical of much of the UK uplands. Topography 150
- is varied with elevations of 180-600 m and the climate is cool with mean 151

annual precipitation of 1180 mm (at Eddleston village, 2011-2017), falling mainly as rainfall. Mean daily temperatures range from 3 **°**C in winter to 13 **°**C. Daily evapotranspiration ranges from 0.2 mm in winter to 2.5 mm in summer (estimated using the Granger-Gray method (Granger and Gray, 1989) using data from the weather station in the catchment at Eddleston village). Bedrock throughout most of the catchment is comprised of Silurian impermeable well-cemented, poorly sorted sandstone greywackes (Auton, 2011). Extensive glaciation has affected the superficial geology and soil types. Soils on steeper hillsides are typically freely draining brown soils overlying silty glacial till, rock head or weathered head deposits. Towards the base of the hillslopes the ground is typically wetter and soils comprise sequences of gleyed clays and peats on sub-angular head deposits or alluvial deposits closer to the river. Land cover is mainly improved or semi-improved grassland on the lower slopes and rough heathland at higher elevations. Forest cover is typically mixed coniferous and deciduous woodland, 152 153 154 155 156 157 158 159 160 161 162 163 164 165 166

concentrated along field boundaries. 167

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The experimental hillslope is located \sim 100-200 m from the Eddleston Water rising to 30 m above the river with a relatively uniform slope of ~9**°**. Soil pit surveys (0.7 m depth) found that soils comprise typically 0.15-0.20 m deep silty cambisols containing numerous sub-angular cobbles up to 60 mm length. Large roots (< 30 mm) were prevalent in the top 0.20 m of the forest soils, with occasional large tree roots and frequent smaller tree roots (<5 mm) present down to the bottom of the soil pits. By contrast, small roots were prevalent in the top 0.20 m of the grassland soils, with no roots identified at the base of the soil pits (Figure S1). Borehole logs (Figure S1) and a grid of initial ERT surveys showed a clear layered structure to the underlying 169 170 171 172 173 174 175 176 177 178

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geology, with soils above a layer of silt/loam glacial till containing numerous large cobbles, which transition at 1.5-2 m depth into sub-angular head deposits or weathered rock head. 179 180 181

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Soils on the hillslope are generally freely draining, although surface runoff was observed at the wettest times of year in the area upslope of the forest strip. Hydraulic conductivity of soils overlying head deposits has been measured as part of the wider project on a similar hillslope 2 km to the north which found median values of 21-39 mm h^{-1} (0.50-0.94 m d⁻¹) for improved grassland and 42 mm h⁻¹ (1 m d⁻¹) for an \sim 50 year old plantation forest, and 119-174 mm h^{-1} (2.86-4.18 m d⁻¹) for broadleaf forests > 180 years old (Archer et al., 2013). The hydraulic conductivity of the glacial till was estimated to range from $<$ 0.001 to 1 m d⁻¹ based on data from other locations in Scotland (MacDonald et al., 2012). Hydraulic conductivities of the underlying head deposits could not be measured directly using falling head tests in the piezometers as values were beyond the design limit of the test methodology (40 m d^{-1}). However, elsewhere in the Eddleston catchment, the permeability of the head deposits has been measured as 500 m d^{1} (O Dochartaigh et al., 2018). Hydraulic conductivity of the bedrock was not measured, but Silurian greywacke aquifers elsewhere in southern Scotland have been shown to have low productivity (Ó Dochartaigh et al., 2015), with an estimated average transmissivity of 20 $m²$ d⁻¹ (Graham et al., 2009). Particle size and organic matter content were determined from soil samples 183 184 185 186 187 188 189 190 191 192 193 194 195 196 197 198 199 200 201 202

taken at 0.15 m and 0.6 m depth at all 14 soil moisture monitoring sites 203

(Table S1). Particle size analysis used the sieving method for the proportion 204

above 2 mm and a Beckmann Coulter LS230 particle size analyser for the 205

proportion below 2 mm, according to international standards (ASTM International, 2004). The soil texture is predominately silty loam with a substantial proportion of gravel and cobbles (22-58% by mass). There is little variation between locations and transects, although the 0.6 m depth sample at the top of the grassland transect and one of the 0.15 m depth samples in the forest strip had slightly higher sand content than the other locations. Organic content was measured for the same samples using the loss on ignition method at 375 °C for 24 hours (Ball, 1964), and was 2-7%. 206 207 208 209 210 211 212 213

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2.2 Experimental setup 215

The experiment consisted of two 64 m instrumented transects established at the same topographic elevation (212-195 m) on the hillslope and separated by 30 m (Figure 1). One transect was on improved grassland, whilst the other intersected, and was centred on, a 14 m wide strip of 27 year old fenced mixed forest containing Sitka spruce (Picea sitchensis), European larch (Larix decidua), ash (Fraxinus excelsior), hawthorn (Crataegus monogyna), oak (Quercus robur) and elder (Sambucus nigra). Tree height ranged from 7 to 14 m and rooting depths were estimated as 0-1.5 m for Sitka spruce and 0-2.5 m for the deciduous trees, based on trees of similar age on similar soils (Crow, 2005; Fraser and Gardiner, 1967). Both land cover types are typical of the wider catchment and much of the UK uplands, with the grassland used throughout the year for grazing sheep and occasionally horses. Fourteen soil moisture sensors (Delta-T SMT150 with GP4 loggers) were 216 217 218 219 220 221 222 223 224 225 226 227 228 229

installed in pairs at 0.15 m and 0.6 m depth at upslope, midslope and 230

- downslope elevations in each transect (3 pairs on the grassland and 4 pairs 231
- on the forest transect). Nine 50 mm-diameter piezometers were installed at 232

2.5 m depth using a hand held rock drill at similar locations to the soil moisture sensors (3 on the grassland and 6 on the forest transect). The additional piezometers on the forest transect were installed close to the upslope and downslope boundaries of the forest. All piezometers were sealed with bentonite to 0.6 m depth and contained a 0.35 m screen at their base. All piezometers were instrumented with non-vented Rugged TROLL 100 loggers logging at 15-minute intervals and levels were checked manually every 3 months. A barometric logger (Rugged BaroTROLL 100) at the site was used to correct for atmospheric pressure. Two tipping bucket rain gauges were installed 16 m upslope and downslope of the forest to check for the influence 233 234 235 236 237 238 239 240 241 242

The logging period was November 2016 to November 2018 inclusive. One of the soil moisture and rainfall loggers failed on the forest transect, resulting in a \sim 5-month data gap for the shallow soil moisture sensor at the top of the transect (F1_15), a \sim 3-month gap in the upslope rain gauge, and a \sim 1-month gap in data for the other three sensors attached to this logger. The groundwater data was also discontinuous due to large seasonal variations in groundwater level leading to water table levels below the level of the sensors. The gaps in data have been taken into account in the analysis where necessary. Additionally, one of the upper soil moisture sensors in the forest (F2b_15) did not respond for any event, perhaps because it was in an air pocket, and was removed from the analysis. Two piezometers (BH_F2b, BH_F3b) which did not respond during the study period were also removed from the analysis. 257 258 259 260 261 262 263 264 265 266 267 268 269

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Two soil temperature probes (Delta-T ST4) were installed at 0.15 m and 0.6 m depth at the top of the grassland transect, and temperature data were also collected from the pressure transducers at 2.5 m depth. Air temperature, wind speed and direction, solar radiation and rainfall data were obtained from an automated weather station 3 km north of the site at Eddleston village and a similar elevation of 200 masl. These datasets were used to estimate evapotranspiration and to infill missing rainfall data as explained in section 2.3.2. Most of the trees closest to the transect in the forest are conifers, but the deciduous trees had no leaves between mid-November and mid-April. 271 272 273 274 275 276 277 278 279 280

Initial 2D ERT surveys consisting of 6 lines at 2 m spacing were carried out in August 2016 across and down the slope to help characterise the geological structure of the site. A series of ten repeated 2D ERT surveys were then 281 282 283

conducted between November 2016 and April 2018 along the forest and grassland transects. The surveys were undertaken using an AGI SuperSting R8 imaging system connected to arrays of 64 stainless steel pin electrodes positioned at 1 m intervals. Measurements were made using the dipole-dipole configuration with dipole sizes (a), of 1, 2, 3 and 4 m and unit dipole separations (n) of 1-8a. Time-lapse inversion of the data was performed using RES2DINV (Loke et al., 2013), which employs a regularised least-squares optimisation approach, in which the forward problem was solved using the finite-element method. 284 285 286 287 288 289 290 291 292

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2.3 Soil moisture and groundwater data analysis 294

The soil moisture and groundwater data were analysed using the whole time series to understand annual changes and through the selection of specific events to understand event dynamics. The whole time series data and event data were also examined on a seasonal basis, with the following definitions: Winter ('Wi': Dec-Feb), Spring ('Sp': Mar-May), Summer ('Su': Jun-Aug) and Autumn ('Au': Sep-Nov), These periods were defined based on the soil moisture data that showed full wetting up did not occur until late Nov-early Dec, providing a better baseline for comparison. 295 296 297 298 299 300 301 302

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2.3.1Whole time series analysis 304

Soil moisture and groundwater level data were first analysed for the whole time series to give an indication of seasonal patterns, discontinuities in the groundwater data and logger errors. Summary statistics included median values; minimum and maximum values; interquartile range; and graphical inspection of wetting up and recession characteristics. Given the discontinuity of the groundwater data, only the proportion of the year for which a water 12 305 306 307 308 309 310

table was recorded and the range in levels were of interest, along with more descriptive details (e.g. recession behaviour) of the water table response to rainfall events. 311 312 313

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2.3.2Event analysis 315

Soil moisture and groundwater events were selected for analysis by first identifying rainfall events and then finding the associated event in the soil moisture/groundwater time series. The rainfall events were selected automatically from the upslope rain gauge time series based on a total event rainfall of ≥ 8 mm and an intensity criterion that an event contained no period longer than 2 hours without rainfall. This resulted in 56 events, which was reduced to 52 events as described in the following paragraph. Characteristics were calculated for each event in the final event dataset, including total rainfall (TR, ranging from 8.2 to 52.6 mm), mean hourly intensity (I, ranging from 0.5 to 2.5 mm h^{-1}), a 5-day weighted antecedent wetness index (AWI, ranging from 1.3 to 48.3 mm) (Kohler and Linsley, 1951) and the 28-day antecedent rainfall (AP28d, ranging from 13.2 to 138 mm). The gap in the upslope rainfall gauge time series from 01/09/2017 – 02/12/2017 was filled directly with data from the weather station at Eddleston village, which was considered appropriate based on the small differences in rainfall recorded across multiple sites in the catchment. A full summary of the selected events is given in Table S2. 316 317 318 319 320 321 322 323 324 325 326 327 328 329 330 331 332

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Events in the time series for the operational 13 soil moisture sensors were initially selected automatically by locating the point after the start of event rainfall where the 1-hour rolling mean smoothed soil moisture exceeded a gradient threshold of $>$ 0.001 m³ m⁻³ h⁻¹ and where the total change in soil 334 335 336 337

moisture was >0.012 m³ m⁻³ h⁻¹. Events in the time series for the seven operational groundwater sensors were selected in the same way but with a gradient threshold of >0.008 m h⁻¹ and where the total change in groundwater level was >0.001 m h⁻¹ in the 1-hour smoothed groundwater data. These thresholds were determined iteratively by graphical inspection of several randomly selected events from each sensor. Saturation behaviour was identified in some of the soil moisture time series as a rapid rise in soil moisture to near saturation, followed by a plateauing in soil moisture and then a rapid decrease in value, which was captured in the algorithm using a combination of the gradient of the rising limb and the maintenance of a peak within 95% of the peak level for more than 1.5 h. 338 339 340 341 342 343 344 345 346 347 348

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Given the variety in types of response, all selected events were inspected manually. Four events were removed completely due to excessive noise, even in the smoothed soil water and groundwater time series, leading to spurious event characteristics across all locations. Further manual adjustments were made for particular locations in some events to adjust start and peak selection due to excessive noise and to correct peaks where very close consecutive events resulted in peak selection associated with the subsequent event. The final event dataset consisted of 52 events (Table S2). 350 351 352 353 354 355 356 357

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The following metrics were calculated for each event, including: whether response occurred in the soil moisture or groundwater data (R); time to response from the start of rainfall (TTR); time to peak from start of rainfall (TTPR); and maximum absolute rise (MR). Response was defined by the criteria above including, in the case of the piezometers, those that rose from an initially dry state. 359 360 361 362 363 364

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Comparison of R, TTR, TTPR and MR between grassland and forest transects was made for a subset of nine events at the wettest points in the time series when the piezometer downslope of the forest responded (and most other sensors were also responding), to enable comparison of sensors with a more balanced design. Pairwise comparisons between sensors in the same domains (upslope, midslope and downslope) and depths on the different transects were also made for all responding sensors in the pair to enable analysis under a wider range of conditions. Tests for normality (Shapiro-Wilk) and homoscedasticity (Fligner-Killeen) were conducted prior to statistical testing. These showed that with a log_{10} transformation the majority of sensor datasets followed a normal distribution and all of them were homoscedastic. Given some deviation from normality but relatively uniform differences in variance, the non-parametric Kruskal-Wallis test was used to compare medians and Dunn's post-hoc test to determine where any significant differences occurred. 366 367 368 369 370 371 372 373 374 375 376 377 378 379 380

Logistic regression was used to test the relationship between event 381

characteristics and whether sensors responded given the binary nature of the data. Spearman's rank correlation was used to assess associations between event characteristics and TTR, TTPR and MR. Prior to the exploration of the relationship between event characteristics and response metrics, co-linearity between the different event characteristics was checked (Table S3). There was some co-linearity between event rainfall and event intensity, and also AWI and AP28d, which was considered in the interpretation of the results. All statistical analyses were conducted in R version 3.5.1 with significance defined as $p < 0.05$. 382 383 384 385 386 387 388 389 390

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2.4 ERT data analysis 392

The ERT surveys were carried out following variable antecedent rainfall conditions (Figure 2). After correction of the ERT model for effects of soil temperature using data from the nested temperature probes (at 0.15 m and 0.6 m depth) and the BH G1 pressure transducer at 2.5 m depth, temporal changes in resistivity between the surveys were assumed to be due to changes in soil moisture content, based on relationships established in other studies (Brunet et al., 2010; Cassiani et al., 2009; Chambers et al., 2014). To factor out potential differences between material properties, comparisons in each of the transects were made relative to the May 2017 survey as it was the driest survey with the highest resistivities. 393 394 395 396 397 398 399 400 401 402

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Resistivity contrasts between depths and locations on the different transects were analysed by averaging resistivities across different lateral or vertical groups of cells in the ERT datasets from each of the transects. Given some deviation from normality in resistivity distributions within groups, median resistivities were compared using the same non-parametric tests as for the insitu sensor data and a bias-corrected bootstrapping procedure used to estimate confidence intervals for each group. 404 405 406 407 408 409 410

3 Results 416

3.1 Seasonal sub-surface hydrological dynamics 417

3.1.1 Soil moisture content and groundwater level 418

Soil moisture content had a distinct seasonal pattern, with generally drier conditions in summer and wetter in winter. This was most pronounced in the shallow soil moisture sensors and lasted longer in the forest compared to the grassland (April to December and April to July, respectively) (Figure 3). Saturation occurred during winter in most of the soil moisture time series on grassland areas as distinct plateaued peaks that also recessed rapidly (Figure 3). In most instances this was due to infiltration, but occasionally at locations F1_60 and G2_60 the water table rose above the level of the soil moisture sensor. Saturated soil moisture conditions were not apparent in the forested areas (F2 sensors). 419 420 421 422 423 424 425 426 427 428

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Soil moisture content in the grassland areas upslope and downslope of the forest strip (F1 and F3 sensors) displayed similar behaviour to those on the grassland transect, with the exception of the 0.6 m depth sensor upslope (F1_60), which had a higher soil moisture content throughout almost the entire time series than the paired grassland sensor (G1_60), possibly due to the location in a shallow topographic depression. The upslope rain gauge had higher daily rainfall than the downslope gauge during the study period (paired t-test, $p < 0.01$), probably due to the prevailing wind direction, but the mean difference was only 0.1 mm d $^{-1}$. 430 431 432 433 434 435 436 437 438

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Figure 3: Time series of a) 15-minute soil moisture (SM) and b) 15- 440

minute groundwater level (GWL) data from the grassland and forest 441

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- **strip transects for the entire study period November 2016-November** 442
- **2018. Soil moisture sensor F2b_15 was poorly responsive and** 443
- **possibly in an air pocket so data are not shown. Note different y-axis** 444
- **scales for GWL data. c) Hourly rainfall data (R) from the upslope rain** 445
- **gauge (aggregated from 15-minute data for clarity).** 446

Over seasonal timescales there was generally more variability in soil moisture content at 0.15 m depth compared to at 0.6 m depth, apart from in the forest strip, where seasonal variability was similar in both shallow and deeper soil depths. This deeper and prolonged drying of the forest soils in summer and

autumn has implications for soil water storage potential. For the whole time series, cumulative soil moisture content was 72-75% and 81-96% compared to a baseline of cumulative median winter soil moisture content for all sensors in the forest (F2 sensors) and all sensors on grassland respectively. An example of this contrast between two sensors is shown in Figure 4. Most of the estimated 15% 'additional' storage capacity in the soil beneath the forest strip occurred in the three months September-November. This is likely to be an underestimate of the actual storage, or the additional storage available in winter, because saturation was not observed in the forest soils during the study period. 452 453 454 455 456 457 458 459 460 461

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Figure 4: Soil moisture content at 60 cm depth under forest (F2a_60) and grassland (G2_60) and for the entire study period compared to the baseline of the median winter soil moisture content for each sensor (horizontal lines). Highlighted areas are the soil moisture deficit in summer/autumn months, indicating the potential soil moisture storage. 463 464 465 466 467 468

Groundwater data were discontinuous at the depths of all the hillslope piezometers. A water table was recorded for much of the study period on the grassland transect and in the upslope part of the forest transect. It was highest during winter but disappeared from all piezometers during midsummer, with a range of over 2 m in some piezometers. In three of the four piezometers with the most continuous data, the water table showed bi-modal recession behaviour, with an abrupt drop in water table depth below a threshold level of 1.87 m below ground level in BH_F1a, 1.50 m in BH_G2 and 2.48 m in BH_G3 (Figure 3). This is indicative of layered geology with large contrasts in permeability between layers, probably representing the transition from less permeable glacial till to unconsolidated gravelly head deposits or weathered rock head. 470 471 472 473 474 475 476 477 478 479 480 481

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3.1.2ERT survey data 483

Resistivity structure along transects 484

The resistivity surveys give insights into the geological structure of the hillslope, with a layered structure visible on both transects (an example is given in Figure 5 and the same structures are visible in Figure S2). Outside the forest strip the topmost layer (0-0.5 m) on both transects had lower resistivities in winter and higher resistivities in summer. This layer corresponds with more organic rich soil according to the borehole logs and soil pits, and sits on a much higher resistivity layer (0.5- 1.7 m) that corresponds with glacial till (Table S1, Figure S1). Below 1.7 m depth, resistivities decreased again, probably due to the presence of a water table in many of the grassland areas on both transects, as the borehole logs do not indicate a significant change in geological properties at this depth. The upslope part of the grassland transect differed from other grassland areas, with higher resistivities below a depth of 0.5 m. The resistivity structure was different in the forested area, with less obvious layering and high resistivities to the bottom of the section. **Figure 5: Resistivity cross section for the grassland (foreground) and** 485 486 487 488 489 490 491 492 493 494 495 496 497 498 499 500

forest (background) transects in November 2016. 501

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Resistivity variation with depth and time along transects 504

The time-lapse ERT data indicate that the variation in resistivity across the ten surveys generally decreased with depth on both transects and at all slope locations (Figure 6). However, variability was greater on the forest transect, particularly to 1.7 m depth within the midslope forest strip area. In this zone interquartile range (IQR) of the relative resistivities was 4.0-16.8 % for the forest and 2.5-6.8 % for the adjacent grassland. Within the first 12 m downslope of the forest, there was also greater variation in relative resistivities in the top 1.7 m depth compared to the adjacent grassland and compared to similar locations upslope of the forest. In this zone the IQR of the relative resistivities was 6.71-12.7 % for the forest and 1.7-10.2 % for the adjacent grassland (Figure 6). The ERT time series data give further insight into the changing seasonal 505 506 507 508 509 510 511 512 513 514 515 516 517

impact of the forest strip on hillslope subsurface hydrological dynamics along 518

the hillslope (Figure 7). In the upslope domain, resistivities displayed similar 519

seasonal patterns on both transects. They were higher in the drier summer surveys compared to the autumn, winter and spring surveys, with the amplitude of the changes decreasing with depth, and little variation below 2.5 m. 520 521 522 523

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The largest differences between transects were in the midslope area. The absolute changes in resistivity between surveys were more pronounced in the midslope forest domain than in the grassland, implying more extreme wetting and drying of the subsurface below the forest strip. The forest area also remained more highly resistive later into the year (through the autumn surveys). This effect was minimal below 2.5 m and insignificant below 3.4 m. 525 526 527 528 529 530 531

The seasonal pattern of changes in resistivity was similar in the downslope domain to the upslope domain, with higher relative resistivities in the summer surveys and lower resistivities in the autumn, winter and spring surveys. There is no indication that the prolonged subsurface drying into the autumn beneath the forested area extended downslope of the forest strip. As in the upslope and midslope domains, the amplitude of seasonal changes decreased with depth on both transects. 532 533 534 535 536 537 538

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Figure 6: Resistivity variation at different depths along the two transects for the 10 surveys conducted between November 2016 and April 2018 relative to the May 2017 survey (horizontal line at 0). The forested area is located within the midslope domain. The horizontal line inside the box represents the median and the lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers depict the largest and smallest values respectively 540 541 542 543 544 545 546

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- **within 1.5 * the interquartile range (IQR). Outliers removed for**
- **clarity. x-axis labels represent range of cells (as distance along the**
- **transect) used to calculate statistics e.g. [0,4) indicates the first**
- **four model cells on the line between 0-1,1-2, 2-3 and 3-4 m.**

Figure 7: Median resistivities for each transect across different

- **domains and depths for the 10 surveys conducted between**
- **November 2016 and April 2018 relative to the May 2017 survey**
- **(horizontal line at 0). The forested area is located within the** 555
- **midslope domain. Median resistivities for each survey are calculated** 556
- **from cells across the whole domain (i.e. 0-24 m for the upslope** 557
- **domain, 24-40 m for the midslope domain, and 40-64 m for the** 558

downslope domain). Shading represents 95% confidence intervals.

groundwater sensors at ~2.5 m depth (Figure 8). However, there were significant differences in the number responding between transects at different locations on the hillslope, when comparing sensors at all depths in each domain. The most significant difference in the number responding was in the midslope domain ($p < 0.001$). 66% of grassland sensors in the midslope domain responded over the 52 events, whilst only 31% responded in the forest strip. Much of the relative decrease in the forest domain was due to fewer of the 0.15 m (particularly in summer) and 2.5 m sensors responding (Figure 8). There was less difference in number responding between the transects in the upslope domain (58% and 74% responded for forest and grassland respectively) and downslope domain (62% and 69% responded for forest and grassland respectively). Some of the difference in the upslope domain can be explained by events not being logged as responses due to soil saturation prior to the event for three events at location F1_60 and one event at F1_15. 566 567 568 569 570 571 572 573 574 575 576 577 578 579 580

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- **Figure 8: Number of sensors responding (%) across all rainfall events**
- **(n=52) for all working soil moisture and groundwater sensors at**
- **different depths and domains on the forest strip and grassland**
- **transects for Winter/Spring (Wi/Sp) and Summer/Autumn (Su/Au)**
- **seasons.**

Comparing data from the nine events when most of the sensors responded, the time taken for sensors to respond (TTR) increased with depth in all domains and there was no significant difference in TTR between forest and grassland transects at any location or depth (Figure 9). However, TTR increased downslope for the piezometers, with significant differences between upslope and downslope locations ($p < 0.05$), but not for the soil moisture sensors (Figure 9). The pairwise comparison of all events (n=52) additionally indicates that there were no significant differences in TTR between summer and winter at any location, although summer TTRs were slightly more variable than winter TTRs (Figure S3). 588 589 590 591 592 593 594 595 596 597

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Figure 9: Time to response from the start of rainfall (TTR) for the different domains and depths on the forest strip and grassland transects during nine rainfall events when the borehole downslope of the forest responded and the majority of the other soil moisture and groundwater sensors responded. The horizontal line inside the box represents the median and the lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers depict the largest and smallest values respectively within 1.5 * the interquartile range (IQR). Numbers in italics show the number of events in which sensor responded. Dots are outliers. 599 600 601 602 603 604 605 606 607 608

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The time that sensors took to reach peak soil moisture/water table from start of rainfall (TTPR) and the maximum rise (MR) were much more variable at individual sensors and between sensors, especially during the subset of nine events in wetter conditions (Figure S4a). This was mainly due to the rapid occurrence of saturation in some of the 0.6 m sensors. However, there appears to be a similar pattern to that seen in the TTR data, of increasing water table TTPR downslope but no systematic increase in soil moisture TTPR. The pairwise comparison of all 52 events suggests that TTPR was seasonally variable, especially in the forested midslope domain. In summer, the TTPR interquartile range for all forest locations was 13-16 hours, compared to 6-11 hours for the adjacent grassland) (Figure S4b). 610 611 612 613 614 615 616 617 618 619 620

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3.2.2 Relationships between event characteristics and 622

subsurface hydrology response metrics 623

Total event rainfall and the 5-day AWI are good predictors of overall number of sensors responding ($p < 0.001$). There are also significant seasonal differences, with the log odds of response much less likely in summer/autumn compared to the winter/spring ($p < 0.001$). Comparison between transects, depths and domains reveals a more complex picture. Total event rainfall and seasonal differences are significant explanatory factors for whether sensors respond to events in most locations (Figure 10). However, event characteristics and seasonal variation in conditions have less impact on the response of the 0.15 m soil moisture sensors, because these respond easily across the whole range of events. The 0.15 m sensor in the forest strip is an exception, where response seems to be significantly affected by total event rainfall and there are significant seasonal differences (in summer/autumn compared to winter/spring) compared to grassland areas. Total event rainfall appears to have a more significant impact on the number of the 0.6 m and 2.5 m sensors that respond in most locations, presumably because a threshold level is required for these to respond. The seasonal variation in these deeper sensors is less clear than at shallower levels, but there are similar patterns between 0.6 m sensors on the forest and grassland lines, with significant differences between summer/autumn, compared to winter/spring on the forest transect. These differences are consistent with seasonal changes in soil moisture being more marked in the forest strip, with a later onset of sensor response. 624 625 626 627 628 629 630 631 632 633 634 635 636 637 638 639 640 641 642 643 644 645

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Figure 10: Graphical representation of significance levels from logistic regression of the number of soil moisture and groundwater 647 648

sensors responding for different transects, domains and depths for different independent variables across all 52 rainfall events. Spring, Summer and Autumn are based on logistic regression comparisons to 649 650 651

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Correlation of event characteristics and response metrics at individual locations showed some significant correlations but no clear pattern could be identified between transects. Correlation coefficients calculated for data for all sensors across both transects showed more generally that total event rainfall appears to be the most important factor controlling MR for both soil moisture sensors and piezometers. Event intensity also appears to be a significant control on TTR and TTPR for both soil moisture sensors and piezometers. Finally, in winter the 5-day AWI appears to be an important factor in controlling the rate of response of the piezometers and AP28d for the maximum rise in the soil moisture sensors (Table S4). 654 655 656 657 658 659 660 661 662 663

4 Discussion 664

4.1 Forest influence on soil moisture and groundwater 665

dynamics beneath the forest strip 666

Pronounced differences in subsurface hydrology characteristics and dynamics were identified between the forest strip area and the grassland areas on both transects from the 2-year monitoring programme based on soil moisture, groundwater and time-lapse ERT measurements. These observations have been used to infer the hydrological processes operating in the hillslope and to devise the conceptual model of these described below. 667 668 669 670 671 672

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The forested area had lower absolute but more variable soil moisture content, higher relative ERT resistivities, a considerably lower water table and less event-driven response of subsurface sensors. In the zone above the water table and within the rooting depth of the trees (\sim 2.5 m), there were reductions in soil moisture levels and in the numbers of sensors responding during events, that extended later into the autumn compared to the grassland. The ERT data show the same seasonal effects and additionally suggest these were contained within the boundaries of the forest. 674 675 676 677 678 679 680 681

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Our conceptual model to explain these findings is shown in Figure 11. We hypothesise that the differences between the grassland (Figure 11a) and the forest strip (Figure 11b) can be attributed to a combination of greater evapotranspiration and canopy interception by trees, and the likely increased infiltration rate of the forest soils and sub-soils due to more extensive rooting systems and their effects on hydraulic conductivity. Studies in the UK have 683 684 685 686 687 688

found that interception losses can range between 25 and 50% of precipitation, with greater losses for summer events and the interception fraction decreasing with increasing rainfall (Johnson, 1995). Conifers and broadleaves can also lose an additional 300-390 mm yr-1 through transpiration (Nisbet, 2005). These findings provide indirect evidence to explain the differences in response of the forest sensors between seasons, sporadic responses during larger summer rainfall events and the delayed 'wetting up' of the forest soils until the onset of larger rainfall events in the late autumn when some trees had also lost their leaves. Median soil hydraulic conductivities in the forest are likely to range from 42-174 mm h-1, based on results from a study investigating similar hillslopes and land uses in the same catchment, which found that tree rooting systems played a significant role in controlling hydraulic conductivity (Archer et al., 2013). We also found that while there were similarities in the soil matrix and horizon depths under the forest and grassland areas, there were differences in rooting systems, with larger roots and deeper rooting systems in the forest compared to the grassland. These differences in hydraulic conductivity likely contribute to the observed lower absolute soil moisture levels in the forest, higher resistivities and the lower water table. 689 690 691 692 693 694 695 696 697 698 699 700 701 702 703 704 705 706 707

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At depths greater than 2.5 m there were no significant observable seasonal impacts of the forest on moisture dynamics (Figure 11b). Piezometer data from the rainfall events indicate that the water table was within 2.5 m of the ground surface for the wettest periods in the year, probably attenuating the seasonal variations in resistivity observed at shallower depths. The zone below 2.5 m is also likely to be at the limit of the rooting depths of the trees, 709 710 711 712 713 714

reducing their impacts on both evapotranspiration and hydraulic conductivity. The lower water table in the forest strip compared to the grassland is one of the most striking differences between the transects (Figure 11). We suggest that this is due to enhanced hydraulic conductivity within forest soils and subsoils, rather than 'pumping' by trees as the effect persists through the winter when evapotranspiration and interception are greatly reduced. 715 716 717 718 719 720

Figure 11: Conceptual model showing the hillslope with (a) the 721

across-slope forest strip and (b) the grassland transects. The major 722

hydrological fluxes are shown in relation to hillslope, land cover and 723

geological structure, with arrow size relating to the size of the flux. 724

ET: evapotranspiration; P: precipitation; TF: throughfall; I: 725

infiltration. Dashed purple lines in (a) delineate zones of differing 726

moisture dynamics in the forest transect: A) zone within rooting 727

depth of trees (~2.5 m) with greater variability in soil moisture, 728

extended seasonal reduction in soil moisture and reduction in event-729

driven response of sensors; B) zone below rooting depth of trees and 730

with seasonal water table that attenuates seasonal variation in 731

moisture dynamics observed at shallower depths; and C) zone with 732

greater variation in moisture dynamics (inferred from ERT data) due 733

potentially to deeper unsaturated zone and wind shadow effect close 734

to trees. Depths of zones are not drawn to scale. 735

These results are consistent with studies at the hillslope scale on the effects of forest planting on soil moisture dynamics. Significant increases in hydraulic conductivity in forest soils have been reported (Archer et al., 2013; Carroll et al., 2004; Ghestem et al., 2011; Wheater et al., 2008), although few studies have examined directly how variations in hydraulic conductivity due to trees affect groundwater levels across hillslopes. Others have demonstrated the seasonal depletion of soil moisture content and groundwater levels due to forest evapotranspiration (Bonell et al., 2010; Greenwood and Buttle, 2014), but there is considerable variability depending on canopy structure, climate and soil and vegetation characteristics (Guswa, 2012). Similar effects of forest planting and removal have been described at the catchment scale, with afforestation/reforestation often leading to a reduction in annual water yield (Bosch and Hewlett, 1982; Brown et al., 2005; Filoso et al., 2017). Recent meta-analysis of the results of catchment studies worldwide has shown the importance of subsurface storage substrate porosity, permeability and unsaturated zone depth, and its relationship to forest cover (Evaristo and McDonnell, 2019) in modulating annual water yield. 737 738 739 740 741 742 743 744 745 746 747 748 749 750 751 752 753

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4.2 Forest influence on downslope soil moisture and 755

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groundwater dynamics

While the forest strip had measurable impacts on the subsurface hydrological conditions beneath the forest, no significant effects were observed downslope in the zone above the water table (<2.5 m depth). There were no significant differences between transects in long-term median soil moisture content or variability at the downslope soil moisture sensors at 0.15 m and 0.6 m depth. 757 758 759 760 761

For the same sensors there was no significant difference in rainfall event metrics. In the ERT data, the more extreme seasonal variation and prolonged summer/autumn drying that was observed beneath the forest at depths of <2.5 m was not observed in the hillslope portions downslope of the forest, even in areas very close to the forest (<2 m from the forest boundary). As shown in Figure 11, we suggest that the forest has only limited seasonal influence on shallow moisture dynamics. We attribute this mainly to the dominance of vertical processes (evapotranspiration and drainage) in the unsaturated zone as in other areas of the slope, as well as the continued infiltration and percolation of any surface and shallow subsurface flow as it moves downslope (Klaus and Jackson, 2018). 762 763 764 765 766 767 768 769 770 771 772

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These findings notwithstanding, the forest did appear to depress groundwater depths downslope. During the wettest periods, groundwater depths were up to 1.7 m lower downslope of the forest compared to depths upslope of the forest, and up to 1.5 m lower compared to similar locations on the grassland transect. However, there is evidence that groundwater connectivity existed between the areas upslope and downslope of the forest during larger events. Time to response in the 0.15 m and 0.6 m soil moisture sensors was similar at all locations on the slope, but increased downslope for the piezometers. These longer response times downslope than upslope in the piezometers are interpreted as an indication that lateral flow processes from upslope to downslope are more important than vertical infiltration in driving groundwater dynamics in this part of the slope and in moving water down the slope through a connected shallow groundwater system. This implies that the forest does not 'interrupt' lateral downslope water table connectivity 774 775 776 777 778 779 780 781 782 783 784 785 786 787

during larger events. This is consistent with findings from studies on 788

catchment scale hydrological connectivity and threshold behaviour (Detty 789

and McGuire, 2010a, 2010b; McNamara et al., 2005). 790

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Lastly, the ERT data show that while median relative resistivities across all surveys were similar between transects in the downslope area, they were more variable at shallow depths (<1.7 m) in the first 12 m downslope of the forest strip, compared to the adjacent grassland and similar locations upslope of the forest strip. This may be indicative of a seasonally variable deeper unsaturated zone in the area immediately downslope of the forest with less attenuation of resistivity due to the seasonal water table. The south-westerly prevailing wind and the north-south orientation of the forest strip means that a rain shadow effect from the forested area could also contribute to such variability. This effect has been observed to extend to \sim 6 m on to adjacent grassland at sites with similar height trees in the UK, particularly in winter when frontal rainfall is accompanied by stronger winds (Wheater et al., 2008). 792 793 794 795 796 797 798 799 800 801 802 803 804

4.3 Implications for flood risk management 805

Our study suggests that in temperate environments forest boundary strips could marginally increase catchment storage due to evapotranspirative 'pumping' and interception by trees that extends to deeper depths and is more prolonged than in grassland areas. However, our results show that this additional subsurface moisture storage is highly restricted in space to the area in and around the forest itself. This effect is greatest in summer and autumn, so may have a mitigating effect on summer flood events, but additional storage capacity is likely to be limited in winter and spring. Such 806 807 808 809 810 811 812 813

effects are also likely to vary with forest type and age, as discussed in other studies (Archer et al., 2013; Chandler et al., 2018; Jipp et al., 1998). Given that flood events commonly have higher frequencies in summer in small catchments in Scotland (Black and Werritty, 1997) and in the immediate region of this study (Masson, 2019), additional subsurface moisture storage provided in summer by forest strips may provide some benefit depending on storm characteristics and antecedent conditions. 814 815 816 817 818 819 820

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At the storm event timescale, our results suggest that forest strips locally decrease the responsiveness of soils and groundwater beneath the forest strip to rainfall events, especially in summer/autumn. During larger rainfall events and in winter, forest soils respond similarly to rainfall events and at similar rates as grassland, but appear to saturate less frequently, suggesting that forest strips could reduce runoff through combined effects of intra-event evaporation and more rapid drainage to the subsurface. This is aligned with reported increased hydraulic conductivity and porosity in soils below forest strips (Carroll et al., 2004; Wheater et al., 2008). 822 823 824 825 826 827 828 829 830

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From this study, the spatial influence of forest strips appears to be slightly larger than their width, with some downslope depression observed in soil moisture content and groundwater levels. In slopes with much less permeable soils or compacted soils, the forest may act more like a "French drain", channelling water into deeper layers. However, the effectiveness of such a system would be limited by the connectivity of the 'drain' to deeper, more permeable substrate, or to more permeable areas laterally, and to the permeability of soils/geology downslope. On its own the limited storage 832 833 834 835 836 837 838 839

capacity of the strip would be quickly overwhelmed if surrounded by a less permeable system. This highlights the highly context-specific nature of the impacts of forest strips on subsurface moisture storage and on the attenuation effects of increases in hydraulic conductivity. 840 841 842 843

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The role of water table connectivity and its links to threshold behaviour in catchment response is increasingly recognised in the hydrological literature (Bracken et al., 2013; Detty and McGuire, 2010a). This study suggests that the forest strip has little impact on groundwater connectivity during larger events, implying that similar upland landscapes with fragmented forest strips might have limited impact on groundwater dynamics at the event timescale and in wetter periods. There is need for further investigation to assess whether there are optimal soil and geological conditions, and extents and locations of forest cover that might have a larger influence at the catchment scale, as has been suggested in other environments (Ilstedt et al., 2016). 845 846 847 848 849 850 851 852 853 854 855

4.4 Conclusions 856

Forest strips are being used around the world for reduction of flood risk. Nevertheless, our knowledge of how forest strips impact runoff in general and local- and down-gradient hydrological conditions, is still poor. This study examined the impact of an across-slope forest strip on sub-surface soil moisture and groundwater dynamics. We found that an increase in soil moisture storage potential associated with the forest strip was highly seasonal and did not extend much beyond the forest strip itself. In this temperate climate, during wetter winter periods, when widespread runoff is typically highest, isolated strips of forest like the one we studied are likely to 857 858 859 860 861 862 863 864 865

have only a marginal impact on sub-surface moisture storage. However, in specific contexts, such as lower magnitude events or intense summer storms, forest strips could locally reduce catchment responsiveness to storm events. This study only considered sub-surface processes; the impacts of forest strips on surface runoff, for example through increased roughness and infiltration, could be greater. 866 867 868 869 870 871

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Our study showed the utility of time-lapse ERT for extrapolating findings from point-based measurements along hillslopes and to greater depths in terrain that is difficult to instrument invasively. ERT helped to show the larger, longer and deeper seasonal changes in soil moisture in the forest compared to adjacent grassland, as well as providing insight into the lateral variability of moisture changes within the transects. Higher frequency ERT data that is now available at daily or sub-daily time-steps (Chambers et al., 2014) would be a useful extension to this study to further understanding of subsurface hydrological dynamics at the storm event scale. 873 874 875 876 877 878 879 880 881

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Supplementary Information on: 1139

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The impact of across-slope forest strips on 1141

hillslope subsurface hydrological dynamics 1142

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Figure S3: Pairwise comparison of soil moisture and groundwater TTR between the two transects and between seasons for all rainfall events analysed (n=52). Pairs are filtered to contain only events when sensors on each transect responded and the event sample size for each pair is denoted in italics. The horizontal line inside the box represents the median and the lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers depict the largest and smallest values respectively within 1.5 * the interquartile range (IQR). Numbers in italics show the number of events in which sensor responded. Dots are 1183 1184 1185 1186 1187 1188 1189 1190 1191 1192

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Table S3: Spearman rank correlation coefficients calculated to 1230

compare relationships between different rainfall event 1231

characteristics. *p < 0.05; * p < 0.01; *p < 0.001.** 1232

				Time to peak from start of rainfall			Maximum absolute rise (MR, $m^3 m^3$		
	Time to response from the start of rainfall (TTR, h)			(TTPR, h)			for soil moisture and m for groundwater level)		
Soil moisture									
	All	Wi/Sp	Su/Au	All	Wi/Sp	Su/Au	All	Wi/Sp	Su/Au
sensors Total rainfall									
(mm) Intensity (mm	0.0286	-0.0043	$0.136*$	$0.151***$	$0.232***$	$0.194**$	$0.295***$	$0.263***$	$0.271***$
h^1	$-0.375***$	$-0.402***$	$-0.375***$	$-0.437***$	$-0.458***$	$-0.365***$	$0.225***$	0.123	$0.175**$
AWI (mm)	0.0596	0.0152	0.0401	0.0121	-0.112	0.0771	0.0142	0.0768	-0.0376
$AP28d$ (mm)	0.0306	0.081	0.0228	-0.000769	0.0627	0.0115	$-0.132**$	$-0.225**$	-0.0614
Piezometers	All	Wi/Sp	Su/Au	All	Wi/Sp	Su/Au	All	Wi/Sp	Su/Au
Total rainfall									
(mm) Intensity (mm	0.0844	0.146	-0.0714	0.121	0.152	0.0501	$0.325***$	$0.287*$	$0.336*$
$h-1$	$-0.262**$	$-0.337**$	$-0.396**$	$-0.309***$	$-0.294*$	$-0.434**$	$0.181*$	$0.241*$	0.0416
AWI (mm)	0.0118	-0.0138	0.0465	$-0.232*$	$-0.39***$	-0.0314	-0.113	-0.169	0.0764
AP28d (mm)	0.00493	-0.0214	0.0614	-0.0755	-0.0677	-0.0686	0.00722	-0.141	0.250

Table S4: Spearman rank correlation coefficients between rainfall event characteristics / antecedent conditions and response metrics for all soil moisture sensors and for all piezometers across both the forest strip and 1233 1234

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(Wi/Sp, n=20) and Summer/Autumn (Su/Au, n=32). * p < 0.05; ** p < 0.01; * p < 0.001.** 1236